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TEMPERATURE REGULATION IN THE PIKA,

*OCHOTONA PRINCEPS*

by



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## ABSTRACT

The pika, *Ochotona princeps*, maintains a high, and relatively stable, body temperature over a wide range of ambient temperatures. Body temperature ranged from 37.9 to 42.7 C over an ambient temperature range of -9.3 to 24.0 C. Hyperthermia and death occurred in two animals after a 2-hour exposure to ambient temperatures of 28-30 C. There is no distinct circadian rhythm of body temperature. In most animals, daily fluctuation in body temperature was less than 1.5 C and the maximum observed was 2.6 C. No differences in the level of body temperature maintained by this species were observed between June and December.

With increasing levels of spontaneous activity, the body temperature of the pika shows a slight increase. In nature, however, pikas avoid hyperthermia by means of precise behavioral thermoregulation in which both duration and level of activity are regulated.

The minimum metabolic rate in the thermal neutral zone ( $T_a = 21-26$  C) was 1.53 cc  $O_2$ /gm.hr and thermal conductance was between 0.096 and 0.050 cc  $O_2$ /gm.hr. C, 143% and 101-53%, respectively, of their predicted weight-specific values.

The daily metabolic energy requirement of this species over an ambient temperature range of -2.0 to 15 C ranged from 31.41 to 49.66 kcal/animal/day. Based on estimates of winter daily energy requirements, assimilation efficiency, and haypile caloric content, there are sufficient energy reserves in haypiles of 2,000 to 3,000 gm to sustain an adult pika for 97 to 146 days.





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## INTRODUCTION

The pika, *Ochotona princeps*, is a member of the family Ochotonidae, which is holarctic in distribution. Pikas are among the smallest representatives of the order Lagomorpha, and occur from Europe to Japan, from the Himalayas to northern Siberia, and in western North America (Haga, 1960). Zonally, *O. princeps* is a boreal species. This diurnal lagomorph inhabits the talus slopes of the Hudsonian Zone primarily, but also enters the Arctic Alpine Zone. Where rockslides extend down into the wooded Canadian Zone, pikas may also penetrate the lower reaches of these slides (Bailey, 1931).

While limited information concerning the ecology of this species is available (Broadbooks, 1965; Severaid, 1955), physiological data are almost nonexistent. Of particular interest is the ability of this species to survive the long, severe alpine winters. Although Hingston (1925) has reported hibernation in a species of Himalayan pika, most of the available evidence (Hayward, 1952; Broadbooks, 1965) suggests that *O. princeps* is active below the snow throughout the winter, subsisting on stores of dried vegetation.

The problem of maintaining homeothermy at low ambient temperatures is of particular concern, because like other small mammals, the pika demonstrates a relatively high surface area to volume ratio. Other factors being equal, heat loss is proportional to surface area in mammals, and thermal conductance, defined as the rate of heat exchange per degree centigrade difference between body temperature and ambient temperature, tends to be greater in small mammals than in large ones



(Bartholomew, 1968). Therefore, at low ambient temperatures, homeothermy is energetically more expensive with decreasing body size.

In the present study, an attempt was made to evaluate the stability and precision of body temperature regulation in *O. princeps* in relation to ambient temperatures encountered in nature, as well as the role of behavior in thermoregulation. Estimation was also made of the daily energy requirements of this species. By conducting physiological measurements both in the field and in the laboratory, this study provides the first known information on the capability of *O. princeps* in temperature regulation.





## MATERIALS AND METHODS

### COLLECTION OF ANIMALS

All pikas used in this study were live-trapped in the vicinity of Gibraltar Mountain, in the Sheep River area, approximately 48 km west of Turner Valley, Alberta. Thirty-two animals of both sexes were used in this study; 20 of them (15 adults and 5 juveniles) obtained during the months of June, July, and September, 1971, and the remaining 12 (all adults) during the months of July and August, 1972. Trapping was done with Sherman traps (35.5 cm x 10 cm x 10 cm) baited with fresh willow leaves.

### CARE OF PIKAS IN FIELD STUDIES

Most of the summer, and all of the winter, outdoor experiments in 1971 were performed on animals retained within a rectangular field pen (Pen A). The pen, consisting of 0.63 cm wire mesh supported on a spruce frame, measured 2.44 x 1.83 m with a maximum depth of 1.37 m at one end, tapering down to a height of 0.91 m at the opposite end of the enclosure. A rockpile measuring approximately 1.8 m in length and 1.5 m in width, and having a maximum depth of 1.1 m, was provided within the pen. During the summer of 1971, this pen was situated at the lower end of the rock-slide from which the animals were trapped, but in the following summer the pen was moved to a position 6.7 m from the laboratory at the Gorge Creek Biological Station, approximately 18 km east of the above site.



For winter outdoor experiments conducted in 1971, Pen A was placed in a remote woodlot on the University of Alberta Edmonton Research Station.

A limited number of summer outdoor measurements were made in 1971, on pikas kept in cages measuring 91.4 x 26.7 x 20.3 cm with plexiglass sides, and wire mesh tops and bottoms. Wooden nest boxes measuring 15.2 x 15.2 x 15.2 cm were provided within these cages, which were also employed to transport pikas from the field to the laboratory.

In the summer of 1972, an additional field pen (Pen B), similar in basic design to Pen A, was constructed from light spruce logs and 1.9 cm chicken wire (Fig. 1). It measured 2.74 x 1.52 m, with a maximum height of 1.52 m at one end, tapering down to a height of 0.91 m at the lower end of the enclosure. Pen B was situated on the rockslide comprising the 1972 summer study area (Fig. 2), which was in close proximity to the field pen site selected in the previous summer.

In the field, captive pikas were fed natural vegetation consisting mainly of willow leaves and various species of grasses *ad libitum*, and water was provided at all times.

#### CARE OF PIKAS IN LABORATORY STUDIES

In the laboratory, animals were housed individually in wire cages measuring 91.4 x 58.4 x 50.8 cm in a walk-in environmental chamber with an ambient temperature ( $T_a$ ) range of 13 to 15 C. Shelter consisted of either wooden nest boxes as described above, or sections of ceramic drain pipe, measuring 29.2 cm in length, and 9.5 cm in diameter. Dried alfalfa and timothy hay, fresh lettuce and apple, and water were provided *ad libitum*, and when they could be obtained, fresh clover and willow leaves



were used to supplement the regular diet. During the first month in captivity, there was a substantial mortality of animals (25 percent dead in an initial sample of 16), but beyond this period, when the pikas had apparently adjusted to laboratory conditions, survival improved.

#### BODY TEMPERATURE ( $T_b$ )

Over 98 percent of  $T_b$  measurements were obtained via radio-telemetry. The temperature transmitter used in this study was hand-constructed, following the circuit diagram described by Wang (1972). Each transmitter, which measured approximately 22 mm x 12 mm (diameter) and weighed 5.0-5.5 grams, was surgically implanted into the abdominal cavity of the pika, while under Nembutal anesthesia (35-45 mg/kg body weight), supplemented with ether (Mallinckrodt, surgical grade). The continuous tone emitted by the transmitter was received on the FM band of a transistor radio (Transonic FM/AM Model FM-1000 and Sony AM/FM Cassette-Corder Model CF-300), and was recorded on tape (Philips 1530 Cassette Recorder and Sony AM/FM Cassette-Corder Model CF-300). The frequency of the emitted tone was temperature dependent. The frequency of the taped signal was determined by comparing it to that of a variable phase function generator (Hewlett and Packard, Model 203A), and was converted to temperature by reference to a specific calibration curve constructed prior to implantation of the transmitter.

In addition to telemetry, a limited number of rectal temperature measurements were made by insertion of a YSI (Yellow Springs Instrument Co.) No. 402 probe approximately 2 cm into the rectum, and reading from a YSI Tele-Thermometer (Model 42SC). In one pika, a test was made for





possible differences in temperature between the abdominal cavity and the rectum. For this purpose, a Tele-Thermometer probe was inserted into the rectum while the animal was under light anesthesia, and the temperature taken. The probe was then quickly removed, and immediately inserted into a 4 mm incision in the abdominal wall for measurement of intra-abdominal temperature.

#### STANDARD MEASUREMENTS OF BODY TEMPERATURE

$T_b$  measurements were made at 60 or 30 min intervals on transmitter-implanted pikas both in the field and in a walk-in environmental chamber in the laboratory. For measurements made in the laboratory, pikas were maintained at a given  $T_a$  for 24 hr, during which time the  $T_b$  recordings were obtained. Most field recordings of telemetered  $T_b$  were made on animals individually retained in the field pens described above. In order to receive and record the radio signal from these animals at a distance of 12-16 m from the field pen, a twin-lead television antenna wire (300 ohm) was woven throughout the rockpile within the pen, and leads were connected to the antenna of a receiver.

In 1972, telemetered  $T_b$  was obtained from two free-ranging pikas after the implantation of transmitters. They were subsequently released into their respective home ranges within 65 hr of initial capture.

All standard telemetered  $T_b$  measurements made in the Sheep River study area were recorded manually, while an automatic recording system was utilized at the Gorge Creek Field Station, the University of Alberta Edmonton Research Station, and in the laboratory. The recording system consisted of a transistor radio and a tape recorder connected to a



microswitch mounted on a kymograph. A metal pointer fastened to the central shaft of the kymograph closed the microswitch for approximately 50 sec once every hour, and thus provided a.c. power to operate the radio and recorder.

#### BODY TEMPERATURE AND ACTIVITY

In the course of obtaining standard measurements of  $T_b$  at regular intervals throughout the day, an attempt was made to record simultaneously the activity of the pika. For purposes of analysis, all activity was initially classified into five discernible categories: inactive below the rocks; active below the rocks; inactive above the rocks (musing); active above the rocks; and feeding. In analyzing activity data the latter two categories were usually combined into "active above the rocks." In most cases it was possible to detect movement below the rocks, because the magnitude of the radio signal picked up on the receiver fluctuated whenever the pika moved. This was caused by changes in the orientation of the radiating coil in the transmitter, relative to the radio receiver antenna.

To record  $T_b$  during different levels of activity, a number of "activity runs" were performed on transmitter-implanted pikas kept in field pens in 1972. During each run, which lasted from 1 to 2 hours in duration, continual surveillance of the rockpile within the pen was maintained from an observation point. In the case of Pen B, observations were made with the aid of binoculars, from a pup tent 16 m from the pen. At the Gorge Creek Field Station, observations were made from a window in the laboratory, 6.7 m from Pen A. During each activity run, the activity



level of the pika was assigned to one of the five categories described above, and the duration of each activity level was determined with a stopwatch. The initial and final  $T_b$  of the pika for each activity level was recorded, with the final  $T_b$  for one activity level becoming the initial  $T_b$  for the subsequent activity level engaged in by the pika.

All of the above behavioral studies were carried out between June and August, 1972; no attempt was made to evaluate the role of behavior in temperature regulation during the winter months.

#### AMBIENT TEMPERATURE ( $T_a$ )

In the field pen studies carried out in the summer and winter of 1971, both a radio-transmitter and a YSI No. 402 Tele-Thermometer probe were inserted below the rocks for measurement of  $T_a$ . In the summer of 1972, however, all  $T_a$  measurements (with the exception of one series of surface  $T_a$  measurements made with a mercury thermometer) were obtained with hand-constructed Tele-Thermometer probes. Each probe consisted of a YSI Precision Thermistor No. 44033 ( $\pm 0.1$  C interchangeability) soldered to a piece of 16 gauge duplex wire 4.6-18.3 m in length. Polyethylene tubing (P.E. 90) and two coats of Insl-X (Insl-X Products Corp., Yonkers, N.Y.) waterproofed and protected the thermistor tip and the adjoining soldered junctions. A plug-in jack was soldered to the opposite end of the wire for insertion into a YSI Tele-Thermometer (Model 42SC). The thermistor sensors of the finished probes were found to be as accurate as a YSI No. 402 Tele-Thermometer probe. Each of the two field pens used in 1972 was provided with two 15.2 m probes, one located in a chamber at the bottom of the rockpile and the other on the surface.



Six additional probes were inserted to varying depths in different locations on the rockslide in the 1972 study area (Figs. 3-7, inclusive). Two of these probes (No. 5 and No. 6) were located in active haypile sites, and because pikas accumulated vegetation on top of the thermistors, the temperatures recorded were obtained at the base of the haypile in each case. The thermistor of probe No. 4 was situated at the greatest depth--approximately 1.4 m below the surface--and was believed to lie at the bottom of the rockslide at that particular point. Probes Nos. 1 and 2 were used to record  $T_a$  below the rocks at depths of 0.8 and 0.9 m, respectively. Probe No. 3 provided surface  $T_a$  data, while a mercury thermometer suspended from a pole 0.8 m above the rocks, provided air temperatures above the surface of the rockslide. Measurements from all six probes could be obtained within 5 min, and periodic measurements were made at 1- or 2-hr intervals. These probes were all within, or adjacent to, the home ranges of the two free-living pikas implanted with radio-transmitters.

#### OXYGEN CONSUMPTION

Oxygen consumption was measured in an open-circuit system using a Beckman G-2 Paramagnetic Oxygen Analyzer connected with a Honeywell strip chart recorder. Eleven adults (body weight > 110 gm) and 5 juveniles (body weight < 110 gm) of both sexes, ranging in weight from 83.4 to 134.5 gm were used. Each animal was placed in a metabolism chamber consisting of a metal gallon paint can equipped with inlet and outlet air ports, and a port for insertion of a YSI thermistor probe for  $T_a$  measurements. This chamber was housed in a constant temperature





cabinet that could be regulated to within  $\pm 0.5$  C of the desired temperature. Air supply to the animal chamber was measured with a Matheson flow meter (Model No. 620-PB), and was maintained constant at 300 cc/min. Water and CO<sub>2</sub> were absorbed from the downstream airflow by passage through a lucite tube containing a mixture of Drierite and Ascarite (Fisher Scientific Company).

Attempts to make animals post-absorptive prior to experimentation were made and abandoned due to the great stress and the subsequent death of one animal after food deprivation overnight. Instead, neither food nor water was provided within the metabolism chamber during each measurement, which lasted 3 hr. Also, oxygen consumption measurements were begun as soon as the animals were brought into the laboratory from the field, approximately 403 km away. The difficulty encountered in simply maintaining the pikas in captivity, and the investment of time and money involved in the initial procurement of the animals seemed to justify both of the above deviations from standard procedures used in estimating basal metabolism. For those individuals which survived in the laboratory, oxygen consumption measurements were repeated after they had been 3 wk to 6 mo in captivity, when they had presumably acclimated to laboratory conditions.  $T_b$  was not measured during oxygen consumption measurements, both to avoid stressing the animals by handling, and because preliminary telemetry results revealed little change in  $T_b$  over a wide range of  $T_a$ 's. Measurements were not made at  $T_a$ 's exceeding 28 C, after two animals died following a 2-hr exposure to temperatures of 28-30 C. The final rectal  $T_b$  was 43.1 C. For each 3-hr measurement period, three minimal oxygen consumption values, each of at least 10 min duration, were calculated,



following the method of Depocas and Hart (1957). The mean of these three values was used as the best estimate of the minimum oxygen consumption (for that measurement period at a particular  $T_a$ ).

#### DETERMINATION OF DAILY ENERGY BUDGET (DEB)

An attempt was made to evaluate the daily energy requirements of adult pikas from continuous 24-hr measurements of oxygen consumption. Most measurements made in July and August, 1972, were conducted on animals within 1 wk of initial capture, when they were presumably not acclimated to laboratory temperatures. A limited number of summer, and all of the winter measurements (obtained in December, 1972) of DEB were made on laboratory-acclimated pikas maintained at a  $T_a$  of  $14.0 \pm 1.0$  C for at least 58 days. The apparatus employed was identical to that described above, with the exception of the metabolism chamber. This consisted of an airtight plexiglass box measuring 37.6 x 25.9 x 30 cm, with inlet and outlet air ports, a port for insertion of a thermocouple lead for  $T_a$  measurement, and a wire screen floor. The thermocouple was connected to a Leeds & Northrup Speedomax W Potentiometer. Food and water were provided *ad libitum* during each measurement. In summer, food consisted of dried alfalfa and timothy hay, carrot, lettuce, and apple. Dried haypile vegetation collected in August from the study area was provided during measurements conducted in December.

$T_a$ 's, ranging from -2.0 to 15 C, were selected to be representative of the seasonal temperatures encountered by pikas beneath the rockslide in the field and were held constant for each measurement period (run). For all summer runs  $T_a$ 's matched measurements obtained below the rockslide



in the Sheep River study area, during the month in which the subjects were captured and removed to the laboratory. For one winter run, the  $T_a$  selected ( $-2.0^{\circ}\text{C}$ ) was close to the mean haypile temperature ( $-2.6^{\circ}\text{C}$ ) obtained by Krear (1965) between November 17 and June 11, in a Colorado talus slope. For most runs, a photoperiod of approximately 9L:15D was maintained. The airflow to the metabolism chamber was kept at a constant rate of 600 cc/min.

The daily oxygen consumption was determined by totalling hourly oxygen consumption values. Two methods yielding comparable results were used to determine hourly oxygen consumption. One technique involved cutting out a section of chart paper along the recording pen tracing above the base line, equivalent to one hour of measurement, and weighing the paper to the nearest 0.1 mg. Oxygen consumption was then determined by comparing this weight with that of a standard area of chart paper equivalent to a unit oxygen consumption value. The other method involved estimating by eye and drawing a best-fitting straight line through each hourly tracing, as a measure of the hourly oxygen consumption. The daily oxygen consumption value was then multiplied by 5.0 (kcal/liter oxygen consumed), the caloric equivalent for a respiratory quotient of 0.90-0.95, as described by Kleiber (1961).

#### STATISTICAL TESTS

Analysis of Variance and Duncan's Multiple Range Test (Steel and Torrie, 1960), as well as the Chi-square and the t-test (Sokal and Rohlf, 1969) were used to compare mean values calculated for  $T_b$  data. For determination of correlation, Spearman's Rank Correlation Coefficient





was computed (Sokal and Rohlf, 1969), and its level of significance evaluated by means of a t-test (Steel and Torrie, 1960). Differences were considered to be statistically significant where the p value was less than 0.05.



## RESULTS

### BODY TEMPERATURE

Altogether, 2,512 standard  $T_b$  measurements were obtained via telemetry at 30 or 60 min intervals, from 13 adult pikas. Of this total, 1,917 measurements were obtained from 11 animals kept outdoors (Table I). Individual variation in  $T_b$  is evident, and ranged from 37.9 to 42.5 C over a  $T_a$  range of -9.3 to 24 C (measured below the rocks). Of these 11 pikas, 5 were males with a mean  $T_b$  of 40.9 C, while the mean  $T_b$  of 6 females in the group was 40.8 C. The mean  $T_b$  of 4 pikas kept in Pen A during June and July, 1971 (40.1 C) was considerably lower than the mean  $T_b$  obtained from 5 pikas monitored in the field in June, July, and August, 1972 (40.9 C). The mean  $T_b$  of a single pika (No. 112) retained in Pen A between November 23, 1971, and April 28, 1972, and monitored between November 23 and December 18, was 40.0 C, over a  $T_a$  range of -9.3 to 6.8 C (measured in the nest chamber via a  $T_a$  transmitter).

Five hundred and ninety-five measurements were obtained from 4 animals kept in a walk-in environmental chamber in the laboratory during June, July, October, and November, 1971. Two of these 4 animals were also used for telemetry studies in the field during June and July, 1971. The mean  $T_b$  of 40.1 C varied from 39.8 to 42.7 C over a  $T_a$  range of 5.6 to 20.1 C. Animals in both outdoor and laboratory groups maintained similar  $T_b$ 's and no differences were observed between June and December.

Rectal temperatures of 6 adult pikas measured in a walk-in environmental chamber in November and December, 1971, and September, 1972,



varied from 38.8 to 40.4 C over a  $T_a$  range of 5.6 to 20.1 C ( $n = 20$ ). Rectal temperatures tended to be consistently lower than abdominal temperatures obtained via telemetry, over the above range of  $T_a$ 's (Fig. 8). In the one pika in which the rectal temperature and the intra-abdominal temperature were measured in rapid succession, the latter was found to be 0.7 C higher than the rectal temperature.

#### BODY TEMPERATURE IN RELATION TO AMBIENT TEMPERATURE

It is evident from Fig. 8 that  $T_b$  is relatively constant over the range of  $T_a$ 's tested in the laboratory. A similar relationship was observed in the field (Fig. 9). The mean  $T_b$  of the pika (No. 112) which was monitored outdoors in November and December, 1971, at the University of Alberta Edmonton Research Station was 39.7 C ( $n = 11$ ) when  $T_a$  was -8.0 to -9.0 C, and 40.5 C ( $n = 22$ ) when  $T_a$  was between 6.0 and 7.0 C. The minimum  $T_b$  recorded for this animal was 39.2 C, and the maximum 41.0 C over a  $T_a$  range of -9.3 to 6.8 C, inclusive.

#### BODY TEMPERATURE IN RELATION TO TIME OF DAY

For most 24-hr measurements,  $T_b$  appeared to be fairly stable throughout the day (Fig. 10). The daily fluctuation of  $T_b$  in most animals was less than 1.5 C and the maximum was 2.6 C. Although the existence of a moderate diurnal rhythm of  $T_b$  is suggested by Fig. 10, the difference between the mean  $T_b$  during the night (2030-0530) and that during the day is only 0.08 C, which is not significant ( $p > 0.05$ ). An



exceptional circadian fluctuation of  $T_b$  was observed in one adult female (Fig. 11).

No significant differences in  $T_b$  exist between animals maintained in the Gorge Creek field pen, the Sheep River field pen, and those individuals free-living in the Sheep River study area. Figure 12A depicts the hourly  $T_b$ 's for one pika (No. 62) obtained over a two-day period, prior to release into its home range in the study area. The circadian fluctuation of  $T_b$  observed in this pika following release (Fig. 12B) differs only slightly from that presented in Figure 12A, while the mean  $T_b$  remains the same.

#### BODY TEMPERATURE IN RELATION TO BEHAVIOR

A slight rise in  $T_b$  was generally observed over a  $T_a$  range of 2 to 28 C, when either the level or the duration of activity was increased (Table II, Figs. 13A & B, 14A & B). During periods of reduced activity,  $T_b$  decreased towards resting levels (Table II, Figs. 13A & B, 14A & B). The maximum fluctuation observed in any one run was 1.0 C developed over a time span of 24 min (pika No. 142, Table II). The magnitude of  $T_b$  fluctuation with respect to duration and level of activity was most pronounced at high surface  $T_a$ 's (Fig. 14B). However, none of the changes in  $T_b$  observed in different behavioral patterns proved to be statistically significant ( $p > 0.05$ ) with respect to resting  $T_b$ . Similar daily behavior patterns and fluctuations in  $T_b$  were observed between captive and free-living animals (Figs. 15, 16).

Pikas appeared to avoid prolonged surface activity at high  $T_a$ 's. A negative correlation was observed between the duration of time spent on





the surface of the rocks in the field pens, and the surface  $T_a$ , over a range of 3 to 27 C ( $r = -0.74$ ,  $p < 0.01$ ). Within that  $T_a$  range, in 77 percent of the observations in which the pikas were active on the surface of the rocks, the mean duration was less than 200 sec. Over a surface  $T_a$  range of 15 to 28 C, the mean duration of time spent on the surface never exceeded 185 sec. In relation to time of day (0530-1930), the duration of time spent above the rocks demonstrated a slight negative correlation ( $r = -0.61$ ,  $p < 0.05$ ).

Between 0930 and 1930, as the surface  $T_a$  increased, the percentage of observations in which the pika was below the rocks increased, and vice versa (Fig. 15). A moderate positive correlation ( $r = +0.77$ ,  $p < 0.01$ ) was obtained between percentage of time spent below the rocks in Pen B and the surface  $T_a$  over the range of 15 to 29 C.

Between 1130 and 1830, pikas in field pens were on the surface of the rocks 41.5 percent of the time during cool, cloudy weather ( $T_a = 5-15$  C), as opposed to 29.7 percent during warm, sunny weather ( $T_a = 20-30$  C) (Fig. 17).

#### AMBIENT TEMPERATURE

Most  $T_a$  measurements made in the rockslide in the Sheep River study area were obtained between 0730 and 2230 (Fig. 18). It is apparent that during the daytime in the summer, pikas had a broad spectrum of  $T_a$ 's available to them. In the afternoon (1230-1730) for example,  $T_a$  on the surface of the rockslide was between 21.2 and 23.2 C, while 1.4 m below the surface (probe No. 4) it was only 6.8 to 7.6 C. With the exception of probe No. 5 which was located beneath a haypile, all  $T_a$  measurements



obtained at varying depths below the rocks were fairly stable over the period studied. A 24-hr record of  $T_a$  in the Sheep River study area is presented to further illustrate the stability of  $T_a$  below the rockslide (Fig. 19).

#### OXYGEN CONSUMPTION

The measurements of minimum oxygen consumption at different  $T_a$ 's showed a wide scatter (Fig. 20) which precluded determination of thermal conductance by the method of linear regression. Instead, the minimal and maximal estimates of thermal conductance were given by fitting two lines by eye (Fig. 20). Estimated maximum thermal conductance was 0.096 cc  $O_2$ /gm.hr. C, and the estimated minimum thermal conductance was 0.050 cc  $O_2$ /gm.hr. C. No thermal neutral zone in pika was obvious, but it probably extended from 21.0 to 26.0 C, inclusive (Fig. 20). The estimated basal metabolic rate (EBMR) derived from values obtained within this  $T_a$  range was 1.53 cc  $O_2$ /gm.hr. No circadian rhythm of metabolism was observed; time of day at which measurements were made appeared to have no measurable effect on oxygen consumption at any given  $T_a$ .

Acclimation state and body size both had an effect on oxygen consumption at different  $T_a$ 's (Fig. 21).

In both adults and juveniles, weight-specific and absolute oxygen consumption of acclimated animals was less than that of non-acclimated individuals of similar body weight. Also, the weight-specific oxygen consumption of non-acclimated and acclimated juveniles generally exceeded that of the non-acclimated and acclimated adults, respectively, even after correction for metabolic size (dividing hourly oxygen consumption values



by body weight  $^{3/4}$ ).

#### DAILY ENERGY BUDGET

Table III summarizes the daily energy expenditure of six adult pikas over a  $T_a$  range of -2.0 to 15.0 C. The mean daily energy expenditure was 36.80 kcal/day, and varied from 31.41 to 49.66 kcal/day.





## DISCUSSION

### BODY TEMPERATURE

It is evident that *O. princeps* maintains a relatively high and stable  $T_b$  over a wide range of  $T_a$ 's. At low environmental temperatures, such as were encountered in the winter field pen, this species does not hibernate, nor does it appear to enter shallow torpor. Furthermore, there is no indication that a distinct circadian rhythm in  $T_b$  is characteristic of the species.

The precision and stability of  $T_b$  is unusual in view of the small size of the species. In the ground squirrel, *Spermophilus richardsoni*, which is three to four times as large as *O. princeps*, the maximum daily fluctuation is as much as 3.5 C in a single individual (Wang, 1972). Absence of a well-defined circadian rhythm is also unusual, because diurnal species of mammals including the guinea pig (*Cavia porcellus*) and various species of *Spermophilus*, typically demonstrate significantly higher  $T_b$ 's during daytime than at night (Folk, 1957; Hudson, 1964). Only a slight indication of this trend was observed in *O. princeps* (Fig. 10). In contrast to the results obtained by Abrams and Hammel (1964) in the laboratory white rat, the lack of a marked rhythm in  $T_b$  in *O. princeps* suggests that the hypothalamic set-point temperature does not vary appreciably between day and night in this species.

Compared to eight other genera of small mammals of comparable size (*Heliohobius*, *Spermophilus*, *Mesocricetus*, *Scalopus*, *Neotoma*, *Rattus*, *Dipus*, *Tachyoryctes*) (Hart, 1971), the  $T_b$  of the pika is 2-5 C higher.



In relation to other species of mammals inhabiting the rockslide terrain, the  $T_b$  of *O. princeps* is generally 2-4 C higher. For example, in the golden-mantled ground squirrel, *Spermophilus (Citellus) lateralis*, the rectal temperature is 37.7 C (Hock *et al.*, 1968); it is 37.6 C in the least chipmunk, *Eutamias minimus* (*op. cit.*); 38.0-38.5 C in the woodrat, *Neotoma cinerea* (Brown, 1968); and 36.4 C in the marmot, *Marmota calligata* (Hock *et al.*, 1968). The higher  $T_b$  of pikas may be attributed to their high EBMR and low thermal conductance observed in this study (see Fig. 20).

High and relatively constant  $T_b$ 's appear to be typical of lagomorphs in general. The mean rectal temperature reported for the varying hare, *Lepus americanus* (Hart and Pohl, 1965) and the eastern cottontail, *Sylvilagus floridanus* (Janes, 1957), is 39.8 C. For the jack rabbits, *Lepus californicus* and *Lepus alleni* (Schmidt-Nielson *et al.*, 1965), it is 39.2 C. Like pikas, varying hares (Hart and Pohl, 1965) and New Zealand rabbits, *Oryctolagus cuniculus* (Gonzalez *et al.*, 1971) regulate their  $T_b$  within narrow limits over a wide range of  $T_a$ 's. The maximum  $T_b$  tolerated by pikas (42.7 C) is slightly lower than that found in the desert dwelling *L. californicus* and *L. alleni* (43.0-44.1 C) (Schmidt-Nielson *et al.*, 1965).

The discrepancy observed between rectal and intra-abdominal temperatures (Fig. 8) is attributed primarily to actual temperature differences between the two sites. Intra-peritoneal temperatures exceeding rectal temperatures have also been found in other mammalian species. In the rat, the highest intra-abdominal temperature recorded by Grayson and Mendel (1956) occurred in the liver, which was 0.8 C above that of the lower abdominal cavity, while the mesenteric temperature averaged



0.6 C higher. In the monkey (*Papio* sp., *Cercopithecus* sp., *Erythrocebus* sp.), liver temperatures were found to be 0.28-0.42 C higher than rectal temperatures (Grayson *et al.*, 1966). The final location of the implanted radio-transmitter within the peritoneal cavity will therefore have some bearing on the magnitude of  $T_b$  recorded. Differences in the intra-abdominal location of the transmitter may be at least partially responsible for some of the individual variations of  $T_b$  observed in this study.

#### BODY TEMPERATURE IN RELATION TO BEHAVIOR

Of all the factors contributing to the variability of  $T_b$  in small mammals, activity is generally regarded as most significant (McNab and Morrison, 1963; Hart, 1971). The  $T_b$  of a homeotherm at a given  $T_a$  is determined by the ratio of heat production (M)/thermal conductance (C) (McNab and Morrison, 1963). The rise in  $T_b$  associated with exercise in homeotherms is due to an increase in M/C (*op. cit.*), as rapid accumulation of metabolic heat cannot be adequately compensated for by concurrent increase of thermal conductance (Hart and Heroux, 1955). Variation in  $T_b$  during activity is particularly evident in small animals owing to their smaller body mass, which results in a more rapid temperature change with increases of metabolism (McNab and Morrison, 1963).

The elevation in  $T_b$  observed during periods of spontaneous activity in the pika is similar to that found in other small mammals (Bartholomew *et al.*, 1957; Morrison *et al.*, 1959; Hudson, 1962; McNab and Morrison, 1963). In *Perognathus longimembris* (Bartholomew *et al.*, 1957),  $T_b$  was observed to rise or fall 1.0 C in less than 10 min, depending on



changes in activity, and in *Sorex cinereus* (Morrison *et al.*, 1959), an average increase in  $T_b$  of 1.1 C was observed between extremes of quiet and very active behavior. Although not statistically significant, the trend of increasing  $T_b$  with increasing level of activity observed in the pika tends to support the supposition that at a given  $T_a$  the elevation of  $T_b$  during exercise is proportional to the level or intensity of work performed (Hart, 1971). This has been particularly well demonstrated in treadmill experiments with the rat (Gollnick and Ianuzzo, 1968), the hamster (Folk and Shellinger, 1954), and the lemming (*Dicrostonyx groenlandicus*) and domestic rabbit (*Oryctolagus* sp.) (Hart and Heroux, 1955).

Elevation of  $T_b$  associated with activity in the pika is most pronounced at high  $T_a$ 's (Figs. 14A and 14B) because the ability to dissipate accumulated metabolic heat to the environment decreases with increasing  $T_a$ . This observation has been documented in the laboratory mouse (Doss and Ohnesorge, 1966), the rat (Hart and Jansky, 1963), and in the lemming and domestic rabbit (Hart and Heroux, 1955).

Inability to dissipate heat has been postulated to be one of the primary factors limiting work capacity at high  $T_a$ 's (Dill *et al.*, 1932). The excellent insulation of the pika (see below), combined with a relatively high resting  $T_b$  which lies within only a few degrees of the upper lethal  $T_b$ , suggests that the quantity of excess metabolic heat that this species can tolerate is extremely limited. This therefore necessitates a very precise balance between level and duration of activity, and prevailing thermal conditions, such that the pika is able to minimize storage of excess metabolic heat in the body while carrying out the daily activities necessary for survival.





That pikas are capable of altering their activity level during the day without experiencing any marked change in  $T_b$  is evident from Figures 15 and 16. Pikas appear to accomplish this by reducing both the duration and frequency of surface activity at high environmental temperatures. As expected, pikas were observed more frequently during the afternoon under cool, overcast weather conditions, than during periods characterized by high surface  $T_a$ 's when thermal stress posed a more serious threat (Fig. 17). A somewhat similar trend was observed in the antelope ground squirrel, *Citellus leucurus*, in which Hudson (1962) noted a 42 percent reduction in surface activity between  $T_a$ 's of 25 and 35 C, and a 69 percent reduction between 25 and 40 C.

By engaging in short bursts of surface activity (less than 3.5 min duration in most cases), followed by retreat to the cooler, thermally more favourable microclimate beneath the rocks (Figs. 18 and 19), pikas avoid hyperthermia during summer. The sharp  $T_b$  to  $T_a$  gradient which exists beneath the rocks throughout the summer enables pikas to dissipate passively to the environment excess metabolic heat incurred while on the surface.

The relatively poor capability of pikas to prevent hyperthermia after exposure in the laboratory to  $T_a$ 's of 28 C or higher is not unexpected, considering that under natural conditions they seldom encounter such high temperatures. In the course of evolution, therefore, it would appear that there has been little selective pressure for the development of efficient physiological mechanisms for coping with high  $T_a$ 's in this species.

Although the role of behavior in temperature regulation during winter was not systematically examined, it was clear that the pika



maintained in the winter field pen from November to April utilized the subnivean environment afforded by the snow cover. This particular animal constructed a maze of tunnels beneath the snow, which has also been described for *O. princeps* in Colorado (Krear, 1965), as well as for the Himalayan pika, *O. roylei* (Kawamichi, 1968). Furthermore, during very cold weather ( $T_a < -10$  C), *O. princeps* was never observed on the surface. When the pika did appear above the rocks during mild weather ( $T_a > -5$  C), it frequently engaged in prolonged "musing" with the body assuming a spherical shape, in which pilo-erection was prominent. This behavioral response was also observed on cold, windy days in summer. Kawamichi (1969) has described a similar postural adjustment in the Japanese pika, *O. hyperborea yezoensis*, which tends to minimize heat loss to a cold environment.

At no time during the course of this study, however, did *O. princeps* appear to bask in the sun as described for *O. hyperborea yezoensis* by Kawamichi (1969). The latter author has observed this behavioral pattern during sunrise and sunset, at which times the pika orients its body towards the sun so as to receive maximum solar radiation. Considering the relatively high and stable resting  $T_b$  of *O. princeps*, there would appear to be little advantage to this type of behavior; at least not during the summer months.

#### OXYGEN CONSUMPTION

The EBMR in pika (1.53 cc  $O_2$ /gm.hr) is 143 percent of the basal metabolic rate (BMR) predicted by its weight (109.3 gm;  $n = 16$ )



according to the formula:  $\text{cc O}_2/\text{gm.hr} = 3.8 W^{-0.27}$  (Morrison *et al.*, 1959). This is a relatively high value in comparison to other mammals of similar body size. The BMR in *Tamias striatus* (87 gm) is 1.03 cc  $\text{O}_2/\text{gm.hr}$  (Wang and Hudson, 1971); 1.04 cc  $\text{O}_2/\text{gm.hr}$  in *Heliophobius kapeti* (89 gm) (McNab, 1966); 1.0 cc  $\text{O}_2/\text{gm.hr}$  in *Cebueilla phymaea* (100 gm) (Morrison and Middleton, 1967); and 0.79 cc  $\text{O}_2/\text{gm.hr}$  in *Neotoma lepida* (110 gm) (Lee, 1963).

In contrast to BMR, the thermal conductance of *O. princeps* is relatively low, as defined by the estimates of its upper and lower limits (Fig. 20). Such estimates were considered to be in conformation with the biological implications of Newton's Law of Cooling, as evidenced by the constancy of  $T_b$  in pika over the  $T_a$  range used for oxygen consumption measurements. The broad dispersion of oxygen consumption values may be considered to be due to four principal factors. Firstly, since the animals were not deprived of food before testing, they may not always have been in a postabsorptive state during measurement. Secondly, the state of acclimation may be different in different individuals. Thirdly, the wide spectra of body weights, and presumably age differences, account at least partially for the large discrepancies in oxygen consumption values at given ambient temperatures. Fourthly, although only the minimum values were used for calculation, it was difficult to ascertain the activity levels in the course of each measurement. The estimate of maximal thermal conductance ( $C = 0.096 \text{ cc O}_2/\text{gm.hr. C}$ ) is 101 percent of the value predicted from the formula  $C = 1.102 W^{-0.505}$  (Herreid and Kessel,



1967), using a mean body weight of 109.3 gm, while the estimate of minimal thermal conductance ( $C = 0.050 \text{ cc O}_2/\text{gm.hr. C}$ ) is 53 percent of the predicted value.

The relatively low thermal conductance in pikas indicates that resting metabolism at ambient temperatures below the lower critical temperature is generally depressed; a maximum saving of 53 percent of the total energy can be achieved based on the minimum estimate of thermal conductance. Such reduction is of distinct advantage for survival in this species which subsists on limited stores of dried vegetation during the winter months (Broadbooks, 1965).

#### DAILY ENERGY BUDGET

The average daily metabolic requirement (ADMR) of *O. princeps* (36.80 kcal/day) between  $T_a$ 's of -2.0 and 15.0 C is 165 percent of the EBMR in this study, and 243 percent of the BMR predicted from the general formula of Kleiber (1961) based on body weight ( $M = 70 W^{0.75}$ ). The ADMR is 139 percent of the value obtained by Johnson and Maxell (1966) for *O. princeps* in Colorado. However, the range of  $T_a$ 's in their study was not given. Furthermore, their methods, which involved measuring the caloric content of haypile vegetation, stomach contents, and faeces, and determining assimilation efficiency using an ash tracer technique, may be questionable. In comparison to the daily energy expenditure of one adult *O. collaris* (127 gm; 37.7 kcal/day) determined by measuring oxygen consumption at 20.0 C (Morrison and Teitz, 1953), the ADMR obtained for *O. princeps*





in this study is extremely close (97.6 percent).

In comparing and interpreting the significance of the daily metabolism values obtained in this study, caution must be exercised. Strictly speaking, the ADMR is not equivalent to the daily energy budget (DEB) of a species, because the former does not take into consideration the factors of tissue production and daily activity pattern (Gorecki, 1969). The cost of production can be largely ignored, however, because approximately 98.3 percent of the energy flow into small mammal populations is expended in metabolism, and the remaining 1.7 percent is used in production (Ryszkowski and Petruszewicz, 1967). In contrast, the cost of activity in free-living small mammals may correspond to 9 to 20 percent of the total energy budget (Pearson, 1960). A precise estimate of the DEB would require a thorough knowledge of daily activity patterns, and the energy costs of the different activities over the range of  $T_a$ 's at which they occur in nature.

Despite the obvious limitations to normal activity, and the failure to duplicate the daily thermal fluctuations characteristic of the normal environment, the values obtained in this study are considered to be reasonable estimates of the minimal daily energy requirements of *O. princeps* at the  $T_a$ 's examined. It is clear (Fig. 18, Table III) that the  $T_a$ 's studied encompassed the range measured below the surface of the rockslide, which presumably approximates the range of temperatures to which pikas have access in summer. Although the extent to which pikas modify the microclimate through burrowing, nest-building, etc. is unknown, it would seem probable that the mean winter



haypile  $T_a$  ( $-2.0$  C) selected for one run is at least within a few degrees of the actual nest temperature.

Although laboratory acclimation would be expected to have some effect on the DEB measurements, this did not seem to be the case with pika No. 80 (Table III). The difference in daily energy consumption between non-acclimated and acclimated states in this animal at  $9.6$  and  $9.8$  C respectively, was only  $2.73$  kcal ( $8.7$  percent).

Differences in the diet of the pika during measurement are also of interest, especially since temperature regulation may be influenced by the quality of the food ingested (Hart, 1971). For instance, the daily energy requirement of pika No. 104 maintained on a laboratory diet at a  $T_a$  of  $4.5$  C was  $5.28$  kcal/day greater than that obtained for the same animal maintained on dried haypile vegetation at a  $T_a$  of  $5.0$  C. Although this may be an indication that the specific dynamic action (SDA) of the two diets differs, the difference may be due, at least in part, to differences in activity level.

If it is assumed that the energy consumption value measured at  $-2.0$  C ( $49.66$  kcal/day) is a reasonable estimate of the minimum DEB for an adult, free-living pika existing under winter conditions, one may speculate on the energy reserves available to this species during the winter months. By knowing the energy requirement and the assimilation efficiency of the animal, together with the caloric value of the food, it is possible to calculate the potential energy reserves in a given quantity of food.

The mean caloric value (gross energy) of 12 haypiles in Colorado was found to be  $4,472$  cal/gm (Johnson and Maxell, 1966). In a study



conducted by Millar (1971) on pika in southwestern Alberta, the haypiles ranged in weight from 400 to 6,000 gm. The mean haypile weight of adult males was  $2,911 \pm 284$  gm, while that of adult females was  $1,973 \pm 291$  gm. If haypile weight is assumed to range from 2,000 to 3,000 gm, and if it is assumed that the caloric values of the Colorado haypiles are comparable to those in southwestern Alberta, the total caloric content for these haypiles ranges from 8,940 to 13,410 kcal.

If it is assumed that the minimum assimilation efficiency (54 percent) reported by Johnson and Maxell (1966) is a reasonable estimate, a daily energy intake of approximately 92 kcal/adult pika is necessary. The above haypiles would thus provide sufficient maintenance energy at a  $T_a$  of  $-2.0$  C for a period ranging from 97 to 146 days. Conversely, if it is assumed that during the winter pikas subsist exclusively on haypile vegetation from November through May inclusive (212 days), then a haypile of approximately 4,360 gm would be required--well above the mean values reported by Millar (1971). However, it is possible that only part of the haypile stores of individual pikas were collected in the field with the remainder being inaccessible beneath the rocks. Moreover, there is limited evidence that *O. princeps* forages beneath the snow (Kreier, 1965), and thus may supplement its winter diet with vegetation obtained away from the haypile. In short, the energy requirement estimates for free-living pikas are highly speculative, and a precise estimate of the winter DEB of this species must await further research involving in-depth winter field studies.



# LITERATURE CITED

- Abrams, K., and H. T. Hammel. 1964. Hypothalamic temperature in unanesthetized albino rats during feeding and sleeping. *Amer. J. Physiol.* 206:641-646.
- Bailey, V. 1931. Mammals of New Mexico. *N. Amer. Fauna* 53:66-67.
- Bartholomew, G. A., and T. J. Cade. 1957. Temperature regulation, hibernation, and aestivation in the little pocket mouse, *Perognathus longimembris*. *J. Mammal.* 38:60-72.
- Bartholomew, G. A. 1968. Energy metabolism. In Gordon, M. S. (ed.), *Animal Function: Principles and Adaptations*. MacMillan, London. Pp. 48-64.
- Broadbooks, H. E. 1965. Ecology and distribution of the pikas in Washington and Alaska. *Amer. Midl. Nat.* 73:299-335.
- Depocas, F., and J. S. Hart. 1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption in open-circuit system and in a short-lag, closed-circuit apparatus. *J. Appl. Physiol.* 10:388-392.
- Dill, D. B., H. T. Edwards, and J. H. Talbott. 1932. Studies in muscular activity. VII. Factors limiting the capacity for work. *J. Physiol.* 77:49-62.
- Doss, D., and F. K. Ohnesorge. 1966. Motilitat und korpertemperatur von mausen in verschiedenen umgebungstemperaturen. *Pfleugers Arch. Gesamte Physiol. Menschen Tiere.* 289:91.
- Folk, G. E., and R. R. Schellinger. 1954. The diurnal rhythm of body temperature in the hamster. *Anat. Rec.* 120:787.
- Folk, G. E. 1957. Twenty-four hour rhythms of mammal in a cold environment. *Amer. Nat.* 91:153.
- Gollnick, P. D., and C. D. Ianuzzo. 1968. Colonic temperature response of rats during exercise. *J. Appl. Physiol.* 24:747-750.
- Gonzalez, R. R., M. J. Kluger, and J. D. Hardy. 1971. Partitional calorimetry of the New Zealand white rabbit at temperatures 5-35 C. *J. Appl. Physiol.* 31:728-734.
- Gorecki, A. 1969. Metabolic rate and energy budget of the striped field mouse. *Acta Theriol.* 14:181-190.
- Grayson, J., and D. Mendel. 1956. The distribution and regulation of temperature in the rat. *J. Physiol.* 133:334-346.





- Grayson, J., M. Irvine, and T. Kinnear. 1966. Observations on temperature distribution in the cardiovascular system, thorax, and abdomen of monkeys in relation to environment. *J. Physiol.* 184: 581-593.
- Haga, R. 1960. Observations on the ecology of the Japanese pika. *J. Mammal.* 41:200-212.
- Hart, J. S., and O. Heroux. 1955. Exercise and temperature regulation in the lemmings and rabbits. *Can. J. Biochem. Physiol.* 33:428-435.
- Hart, J. S., and L. Jansky. 1963. Thermogenesis due to exercise and cold in warm- and cold-acclimated rats. *J. Biochem. Physiol.* 41:629-634.
- Hart, J. S., H. Pohl, and J. S. Tener. 1965. Seasonal acclimatization in varying hare (*Lepus americanus*). *Can. J. Zool.* 43:731-744.
- Hart, J. S. 1971. Rodents. In Whittow, G. C. (ed.), *Comparative Physiology of Thermoregulation. II. Mammals*. Academic Press, New York. Pp. 2-130.
- Hayward, C. L. 1952. Alpine biotic communities of the Uinta Mountains, Utah. *Ecol. Monogr.* 22:93-118.
- Herreid, C. F., II, and B. Kessel. 1967. The thermal conductance in birds and mammals. *Comp. Biochem. Physiol.* 21:405-414.
- Hingston, R. W. G. 1925. Animal life at high altitudes. *Ann. Rept. Smithsonian Inst.* 1925, pp. 337-347.
- Hock, R. J., J. S. Hart, and P. R. Morrison. 1968. Metabolism (edited by Altman, P. L.), pp. 327-332. *Fedn. Am. Soc. Exp. Biol.*, Bethesda, Maryland.
- Hudson, J. W. 1962. The role of water in the biology of the antelope ground squirrel *Citellus leucurus*. *Univ. Calif. Berkeley, Publ. Zool.* 64:1-51.
- Hudson, J. W. 1964. Water metabolism in desert mammals. In Wayner, M. J. (ed.), *Thirst*. Pergamon, Oxford. Pp. 211-235.
- Janes, D. W. 1957. Body temperature in the eastern cottontail. *J. Mammal.* 38:137.
- Johnson, D. R., and M. H. Maxell. 1966. Energy dynamics of Colorado pikas. *Ecology* 47:1059-1061.
- Kawamichi, T. 1968. Winter behavior of the Himalayan pika, *Ochotona roylei*. *J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool.* 16:582-594.
- Kawamichi, T. 1969. Behavior and daily activities of the Japanese pika, *Ochotona hyperborea yesoensis*. *J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool.* 17:127-151.



- Kleiber, M. 1961. The Fire of Life. John Wiley & Sons, New York. 454 pp.
- Krear, H. R. 1965. An ecological and ethological study of the pika (*Ochotona princeps saxatilis* Bangs) in the Front range of Colorado. Ph.D. Thesis, Univ. of Colorado, Boulder. 329 pp.
- Lee, A. K. 1963. The adaptations to arid environments in wood rats of the genus *Neotoma*. Univ. Calif. Publ. Zool. 64:57-96.
- McNab, B. K., and P. Morrison. 1963. Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. Ecol. Monogr. 33:63-82.
- McNab, B. K. 1966. The metabolism of fossorial rodents: a study of convergence. Ecology 47:712-733.
- Millar, J. S. 1971. Breeding of the pika in relation to the environment. Ph.D. Thesis, University of Alberta, Edmonton. 94 pp.
- Morrison, P. R., and W. J. Teitz. 1953. Observations on food consumption and preference in four Alaskan mammals. Arctic 6:52-57.
- Morrison, P. R., F. A. Ryser, and A. R. Dawe. 1959. Studies on the physiology of the masked shrew *Sorex cinereus*. Physiol. Zool. 32: 256-271.
- Morrison, P. R., and E. H. Middleton. 1967. Body temperature and metabolism in the pigmy marmoset. Folia Primatol. 6:70.
- Pearson, O. P. 1960. The oxygen consumption and bioenergetics of harvest mice. Physiol. Zool. 33:153-160.
- Ryszkowski, L., and K. Petrusewicz. 1967. Estimation of energy flow through small rodent populations. In Petrusewicz, K. (ed.), Secondary Productivity of Terrestrial Ecosystems, Vol. I. IBP Symposium, Poland. Pp. 125-146.
- Schmidt-Nielson, K., T. J. Dawson, H. T. Hammel, D. Hinds, and D. C. Jackson. 1965. The jack-rabbit - a study in survival. Hvalradets Skrifter 48:125-142.
- Severaid, J. H. 1955. The natural history of the pikas (Mammalian genus *Ochotona*). Ph.D. Thesis, Univ. of California, Berkeley. 820 pp.
- Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco. 776 pp.
- Steel, R. G. D., and T. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill, New York. 481 pp.
- Wang, L. C. H., and J. W. Hudson. 1971. Temperature regulation in normothermic and hibernating eastern chipmunk, *Tamias striatus*. Comp. Biochem. Physiol. 38:59-90.



Wang, L. C. H. 1972. Circadian body temperature of Richardson's ground squirrel under field and laboratory conditions: a comparative radio-telemetric study. *Comp. Biochem. Physiol.* 43A:503-510.



## T A B L E S





Table II. Behavioral Observations and Body Temperature Changes in *O. princeps*

Pika No.	Date (Time)	T <sub>a</sub> Surface / T <sub>a</sub> Below	Description of activity	Duration	Initial-final T <sub>b</sub> (°C)
60	July 14, 1972 (1655-1707)	21.0/13.8	Active among the rocks throughout the measurement; intermittent periods of musing and feeding	12 min, 19 sec	38.7-39.5
60	July 15, 1972 (1135-1205)	28.6/14.9	Below rocks - inactive throughout the measurement	30 min	39.6-38.8
60	July 19, 1972 (1616-1630)	16.5/7.6	Initially below rocks - active; appeared on surface - feeding; intermittent periods of musing and moving among rocks	13 min, 29 sec	39.2-39.8
60	July 22, 1972 (1200-1214)	17.2/8.5	Initially below rocks - inactive; appeared on surface - active among rocks; feeding; intermittent periods of musing	14 min	38.8-39.6
142	June 24, 1972 (1617-1641)	12.1/8.8	Initially below rocks - inactive; appeared on surface - musing; intermittent feeding and moving among rocks	24 min, 29 sec	40.9-41.9



Table I. Telemetered Body Temperatures of *O. princeps* Obtained  
in the Field 1971-1972

Pika No.	Sex	Mean body weight (gm)	Month/year measurements obtained	N	Body temperatures recorded (°C)	
					Range	Mean
322	Male	132.0	June, 1971	18	39.5-41.7	41.0
324	Female	132.0	July, 1971	82	39.6-41.8	40.8
1046	Female	132.0	July, 1971	40	38.8-40.3	39.4
325	Female	148.0	June, 1971	61	37.9-40.5	39.4
144	Male	126.6	June, 1972	53	40.1-42.2	41.5
142	Female	134.4	June, 1972	301	40.4-42.5	41.7
60	Male	127.9	July-August, 1972	225	38.5-40.7	39.2
62*	Male	146.2	July-August, 1972	326	41.1-42.4	41.6
68*	Female	128.7	July-August, 1972	86	39.6-41.3	40.5
111**	Male	140.1	November, 1971	103	39.4-41.8	41.1
112**	Female	123.9	November-December, 1971	622	39.2-41.0	40.0
					$\bar{X}$	40.6

\*These pikas were free-living in the Sheep River study area.

\*\*These animals were maintained at the University of Alberta Edmonton Research Station; all other measurements are from pikas in the Sheep River area.



Table III. The Daily Energy Requirements of *O. princeps*

Pika No. and state of acclimation*	Mean body weight (gm)	Date of measurement	Food	Metabolic chamber ambient temperature (°C)	Daily energy expenditure (kcal/day)
46 - Acclimated	146.5	Dec. 21-22, 1972	Dried haypile vegetation	-2.0	49.66
80 - Non-acclimated	126.8	Aug. 16-17, 1972	Dried alfalfa and timothy, carrot, lettuce, apple	9.6	31.41
80 - Acclimated	140.8	Oct. 12-13, 1972	Dried alfalfa and timothy, carrot, lettuce, apple	9.8	34.14
82 - Non-acclimated	115.2	Aug. 17-18, 1972	Dried alfalfa and timothy, carrot, lettuce, apple	9.7	38.61
104 - Acclimated	112.2	June 27-28, 1972	Dried alfalfa and timothy, carrot, lettuce, apple	4.5	38.91
104 - Acclimated	116.0	Dec. 26-27, 1972	Dried haypile vegetation	5.0	33.63
142 - Non-acclimated	114.7	June 26-27, 1972	Dried alfalfa and timothy, carrot, lettuce, apple	11.3	32.60
142 - Non-acclimated	117.6	July 3-4, 1972	Dried alfalfa and timothy, carrot, lettuce, apple	14.0	33.92
144 - Non-acclimated	113.0	June 29-30, 1972	Dried alfalfa and timothy, carrot, lettuce, apple	4.5	40.89
144 - Non-acclimated	113.4	July 4-5, 1972	Dried alfalfa and timothy, carrot, lettuce, apple	15.0	34.20

\*Non-acclimated pikas - in lab one week or less prior to measurement; acclimated pikas - in lab 8 weeks or more, prior to measurement.



## FIGURES





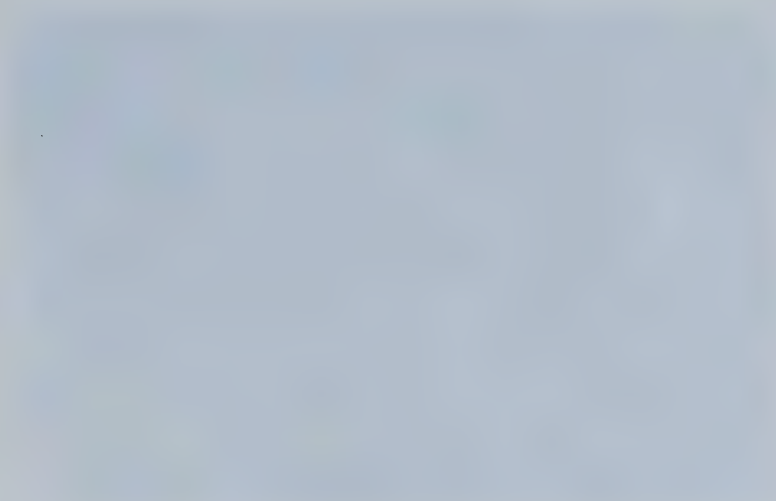
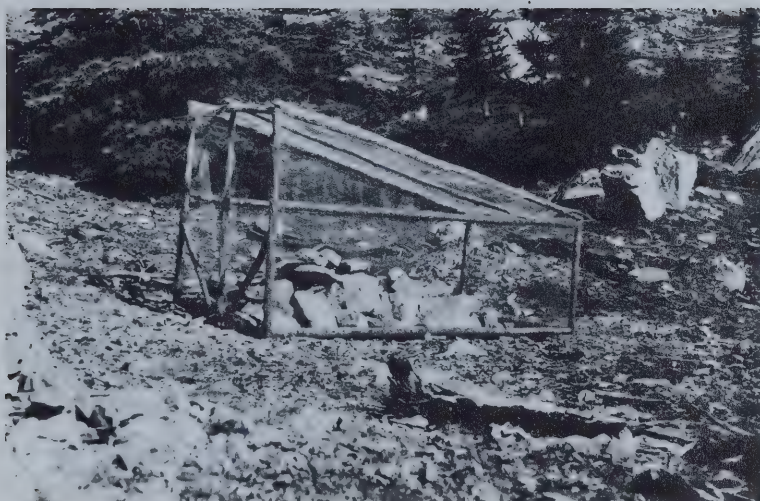


Figure 1. Field Pen B used in Sheep River study area, 1972

Figure 2. Sheep River study area, 1972. Arrow indicates the location of Field Pen B on the rockslide.





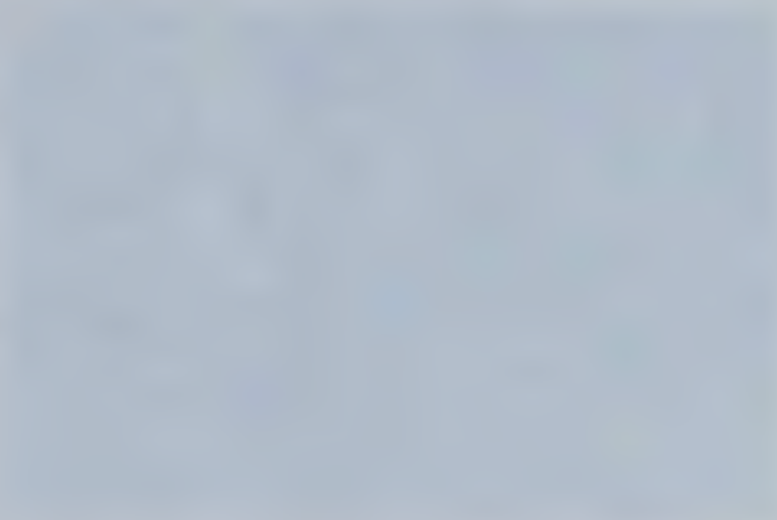


Figure 3. Location of ambient temperature probe No. 1 in the Sheep River rockslide. Arrow indicates the site of probe placement.

Figure 4. Location of ambient temperature probes Nos. 2 (a) and 3 (b). Arrows indicate the sites of probe placement.









Figure 5. Location of ambient temperature probe No. 4 in the Sheep River rockslide. Arrow indicates the site of probe placement.

Figure 6. Location of ambient temperature probe No. 5 in the Sheep River rockslide (active haypile site). Arrow indicates the site of probe placement.







Figure 7. Location of ambient temperature probe No. 6 in the Sheep River rockslide (active haypile site). Arrow indicates the site of probe placement.









Figure 8. Rectal and telemetric abdominal temperatures of *O. princeps* at different ambient temperatures in the laboratory.

O - Rectal temperature (N = 6; 20 measurements)

● - Mean abdominal temperature (N = 4; 347 measurements)

N represents the number of individuals.

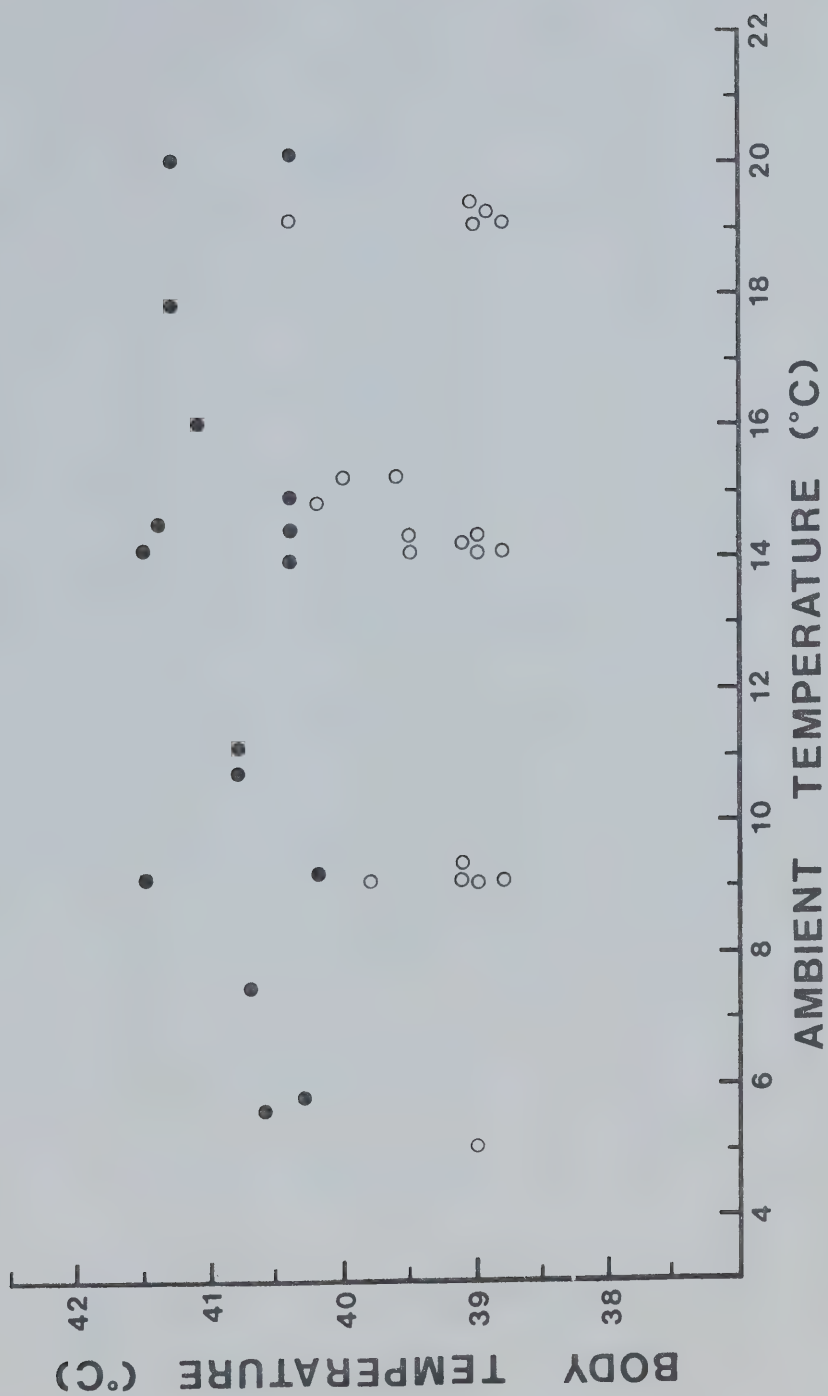






Figure 9. Body temperature of *O. princeps* at different ambient temperatures in the Sheep River study area, 1971-1972 (N = 5; 400 measurements). Vertical lines indicate the range; horizontal lines the mean. Rectangular boxes define the 95 percent confidence limits of the means. Numbers below vertical lines indicate the number of measurements. N represents the number of individuals.

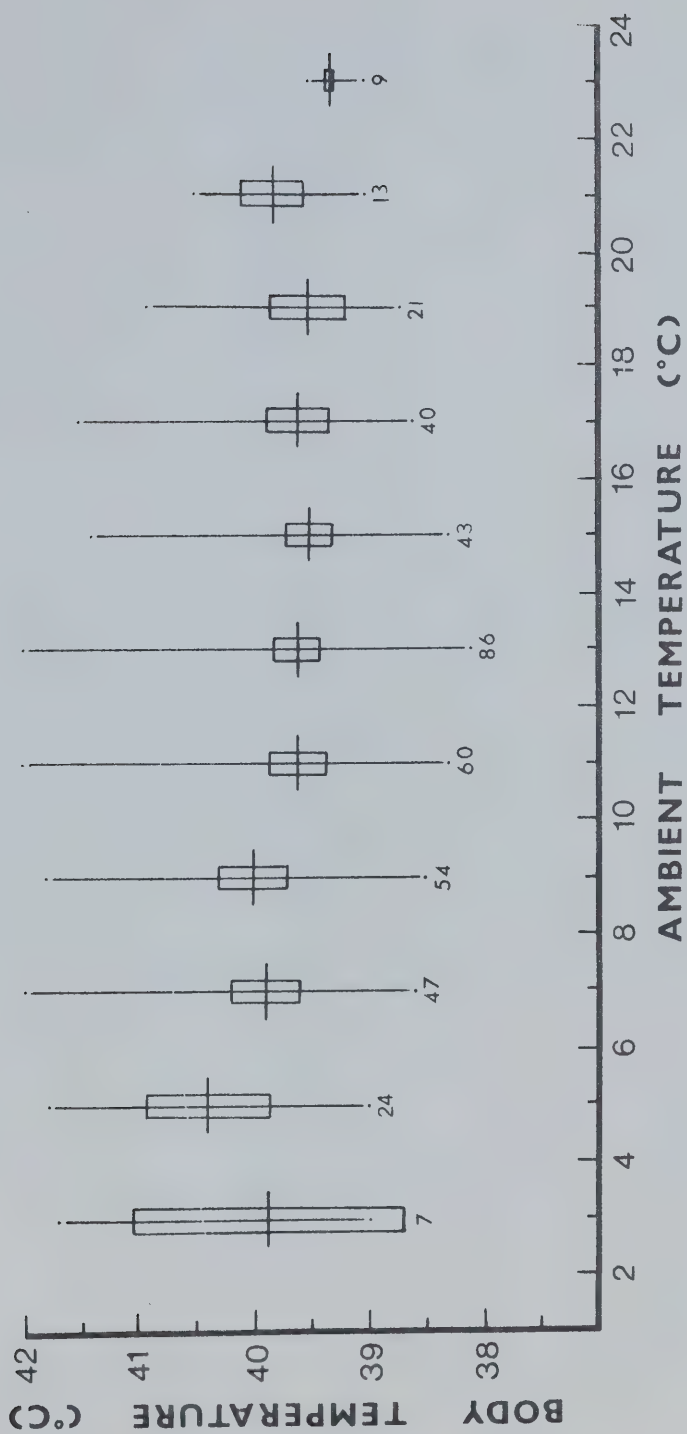








Figure 10. Hourly recordings of body temperature in *O. princeps*.

Measurements are from free-living (2) and captive animals (5) in the Sheep River study area, 1971-1972 (N = 7; 802 measurements). Vertical lines indicate the range; horizontal lines the mean. Rectangular boxes define the 95 percent confidence limits of the means. Numbers below vertical lines indicate the number of measurements. N represents the number of individuals.

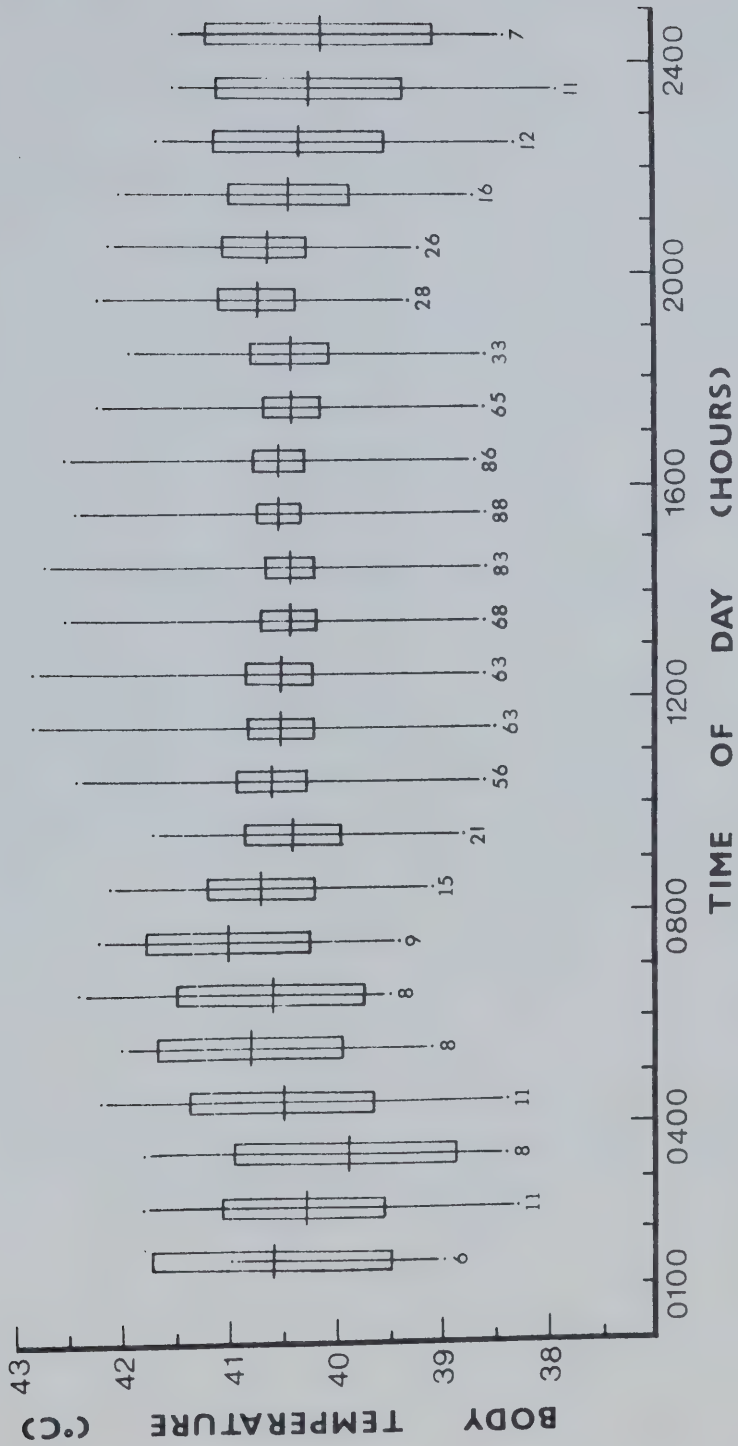






Figure 11. An exceptional circadian body temperature fluctuation of a single adult female pika. The animal was retained in a field pen located in the Sheep River study area, June 20-21, 1971.

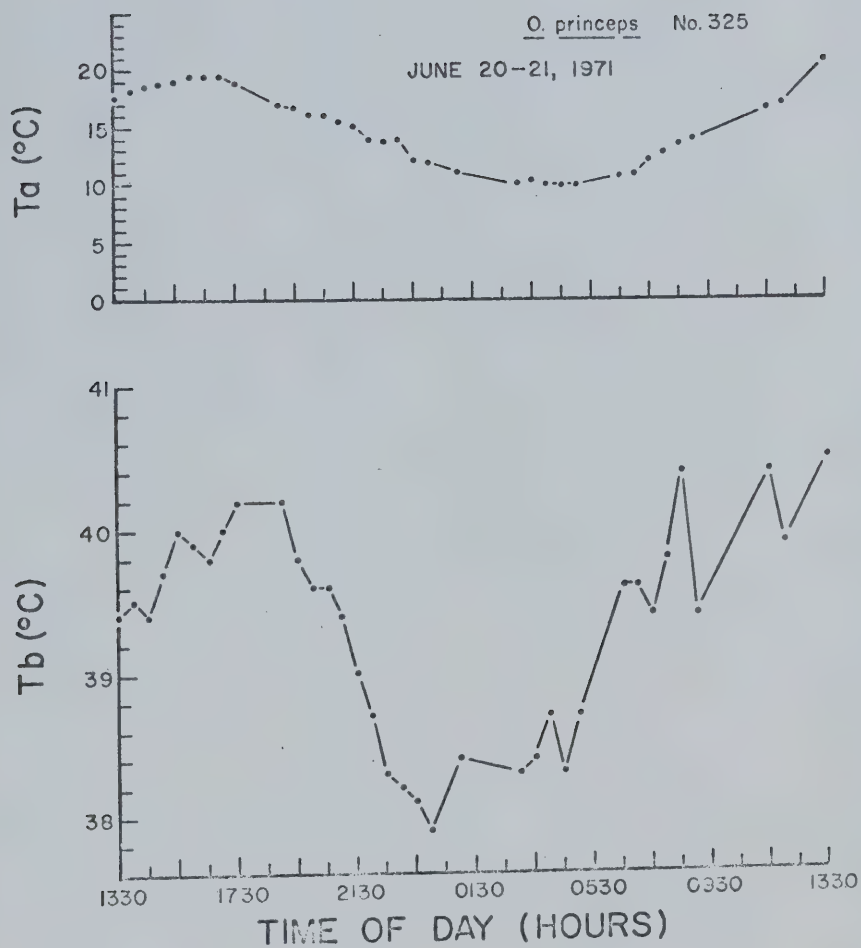


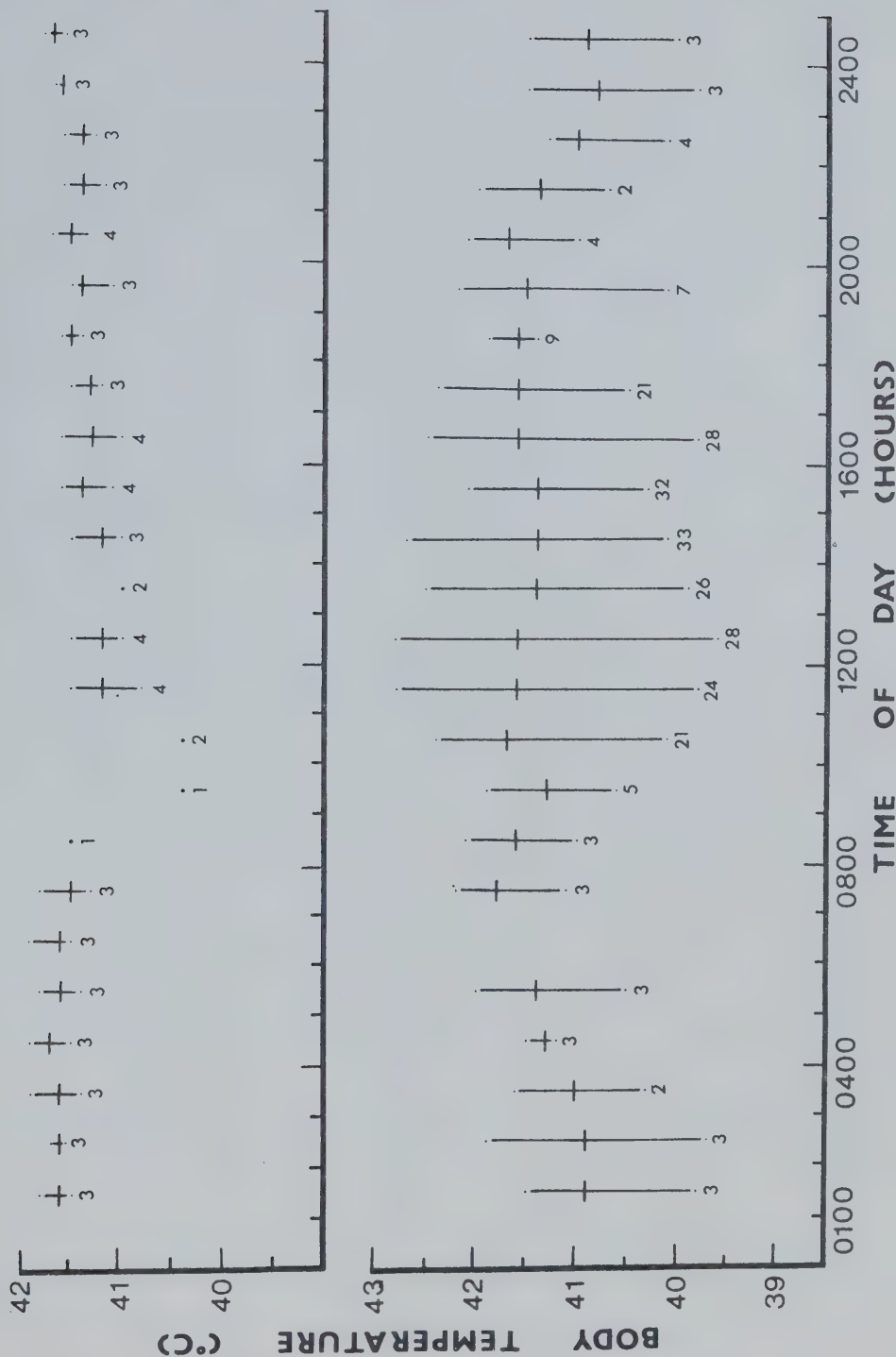






Figure 12A (Upper). Hourly recordings of body temperature of pika No. 62 maintained in an outdoor pen at Gorge Creek, July 17-19, 1972 (71 measurements). Vertical lines indicate the range, horizontal lines the mean. Numbers below vertical lines indicate the number of measurements.

Figure 12B (Lower). Hourly recordings of body temperature of pika No. 62, free-living in the Sheep River study area, July 19-August 11, 1972 (272 measurements). Vertical lines indicate the range, horizontal lines the mean. Numbers below vertical lines indicate the number of measurements.





Date	Description	Amount	Balance	Interest	Total	Notes	Remarks
1900	Jan 1						
1901	Feb 1						
1902	Mar 1						
1903	Apr 1						
1904	May 1						
1905	Jun 1						
1906	Jul 1						
1907	Aug 1						
1908	Sep 1						
1909	Oct 1						
1910	Nov 1						
1911	Dec 1						
1912	Jan 1						
1913	Feb 1						
1914	Mar 1						
1915	Apr 1						
1916	May 1						
1917	Jun 1						
1918	Jul 1						
1919	Aug 1						
1920	Sep 1						
1921	Oct 1						
1922	Nov 1						
1923	Dec 1						
1924	Jan 1						
1925	Feb 1						
1926	Mar 1						
1927	Apr 1						
1928	May 1						
1929	Jun 1						
1930	Jul 1						
1931	Aug 1						
1932	Sep 1						
1933	Oct 1						
1934	Nov 1						
1935	Dec 1						
1936	Jan 1						
1937	Feb 1						
1938	Mar 1						

Figure 13A (Upper). Body temperature changes in pika No. 60 during an activity run, July 22, 1972 (1200-1239).  $T_a$  surface = 17.0 C,  $T_a$  below rocks = 8.8 C.

- a-b - Below rocks - inactive
- b-c - Feeding
- c-d - Active among rocks
- d-e - Musing (in sun); occasional movement
- e-f - Active among rocks; feeding
- f-g - Below rocks
- g-h - Musing (in sun)
- h-i - Active among rocks; intermittent musing
- i-j - Below rocks - inactive

Figure 13B (Lower). Body temperature changes in pika No. 60 during an activity run, July 13, 1972 (1210-1255).  $T_a$  surface = 20.5 C,  $T_a$  below rocks = 12.3 C.

- a-b - Feeding; active among rocks
- b-c - Active among rocks
- c-g (inclusive) - Below rocks - inactive

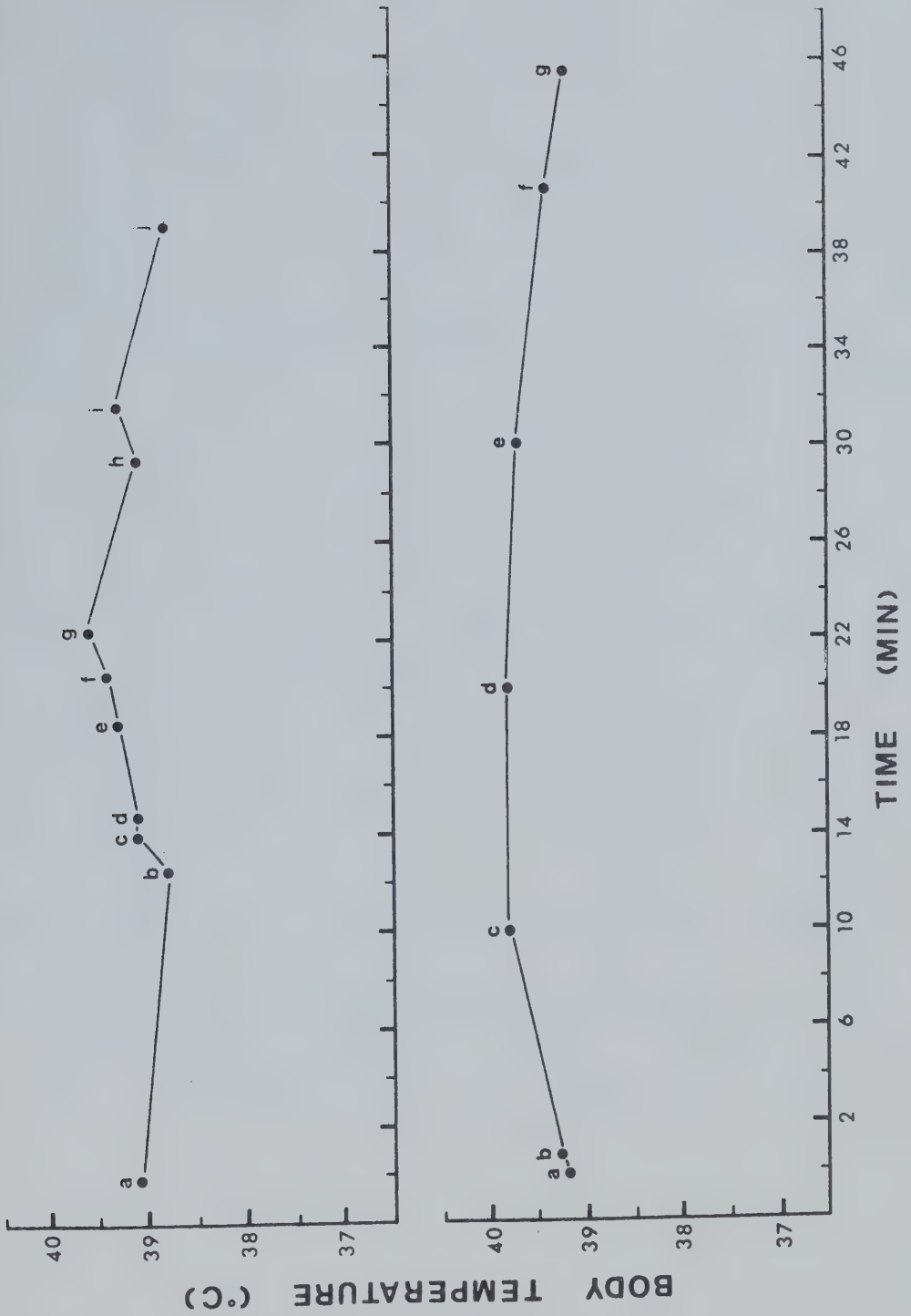








Figure 14A (Upper). Changes in body temperature of *O. princeps* with increasing duration of activity above the rocks (●) and inactivity below the rocks (○) over a surface ambient temperature range of 2-15 C. Numbers above or below points indicate the number of measurements.

Figure 14B (Lower). Changes in body temperature of *O. princeps* with increasing duration of activity above the rocks (●) and inactivity below the rocks (○) over a surface ambient temperature range of 15-28 C. Numbers above or below points indicate the number of measurements.

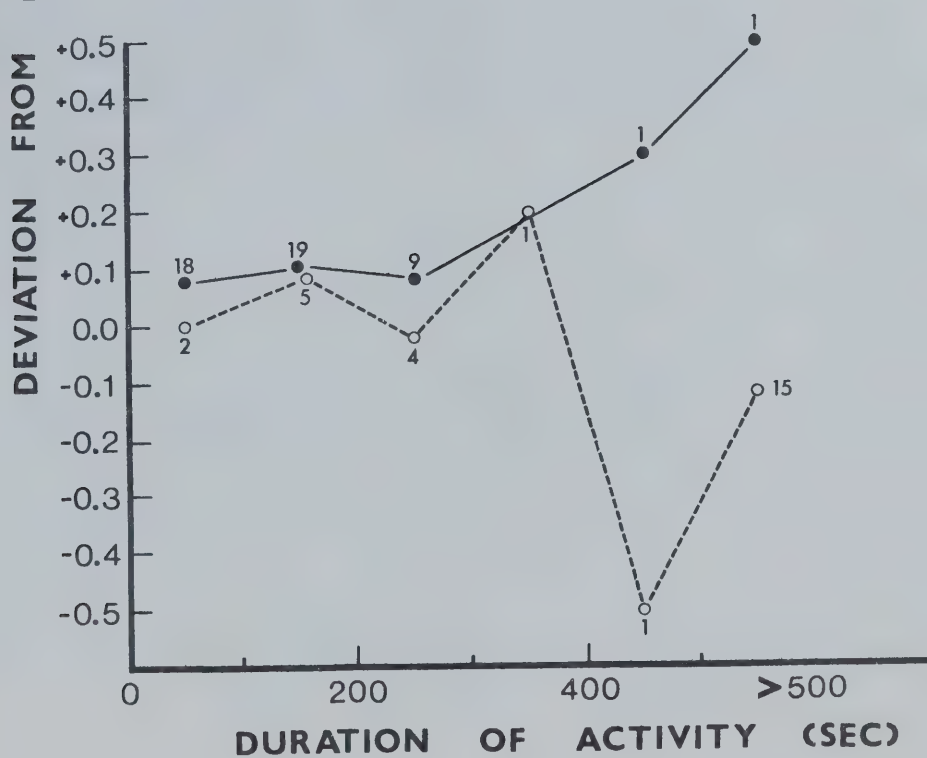
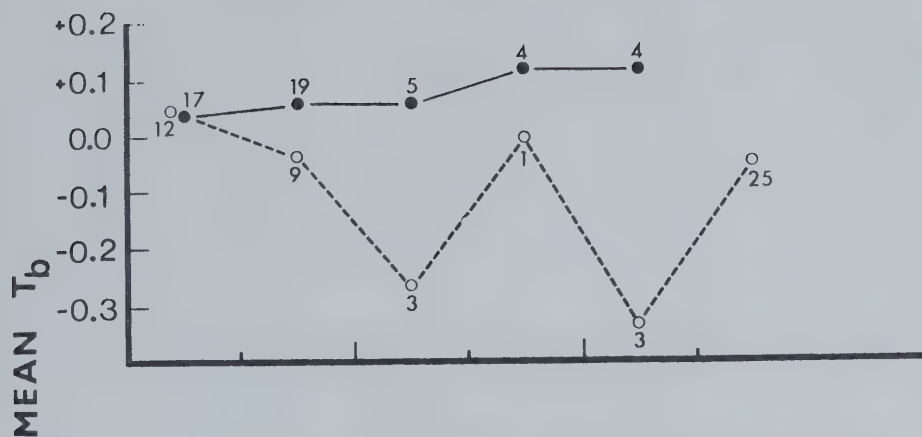






Figure 15. Activity pattern and body temperature fluctuations of *O. princeps* in relation to time of day and ambient temperature (N = 2; 259 measurements). Field pen B, Sheep River study area, June 18-21; July 12-August 9, 1972.

- - Below rocks
  - - Above rocks - inactive
  - △ - Above rocks - active
  - - Surface ambient temperature
  - - Ambient temperature below rocks
  - .... - Body temperature fluctuations - Pika No. 144
  - - Body temperature fluctuations - Pika No. 60
- N represents the number of individuals.

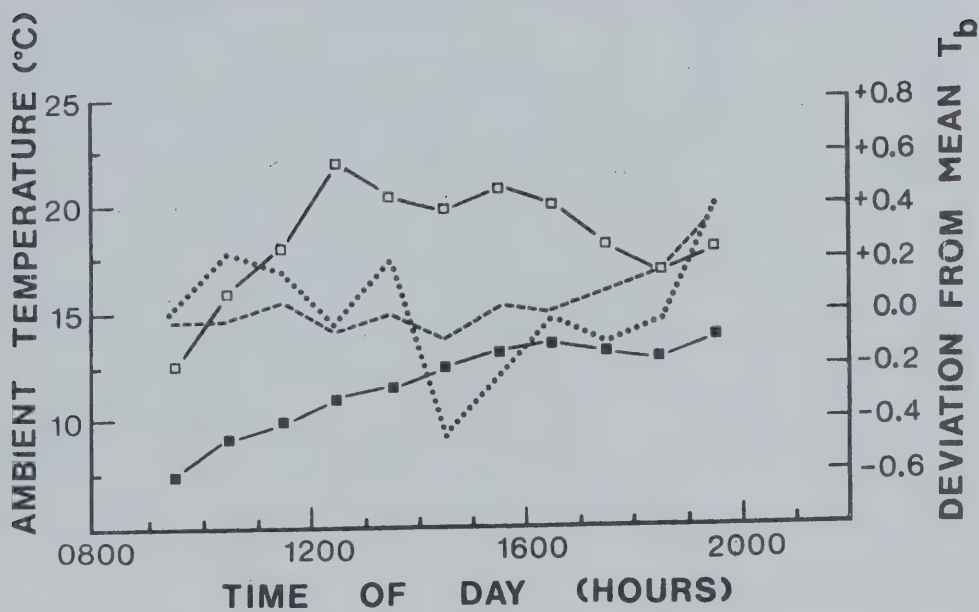
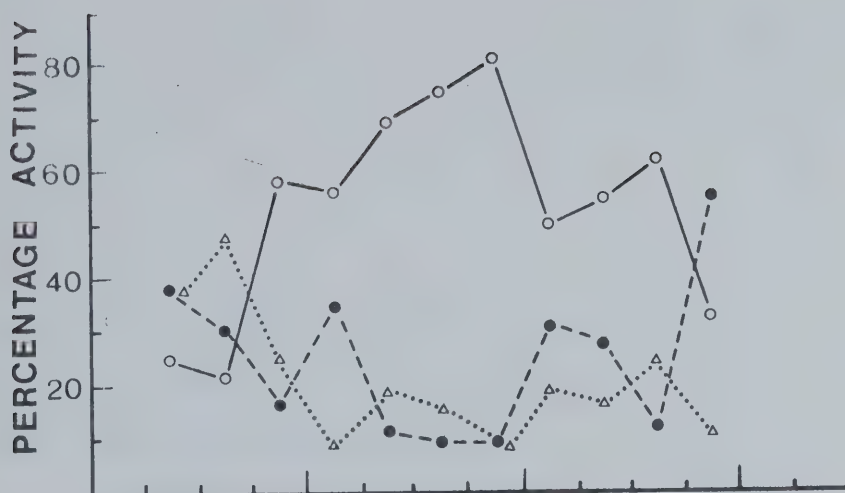








Figure 16. Activity pattern and body temperature fluctuations in free-living *O. princeps* in relation to time of day and ambient temperature (N = 3; 337 measurements). Sheep River study area, July 19-August 11, 1972.

- - Below rocks
  - - Above rocks - inactive
  - △ - Above rocks - active
  - - Surface ambient temperature
  - - Ambient temperature below rocks
  - ..... - Body temperature fluctuations - Pika No. 68
  - - Body temperature fluctuations - Pika No. 62
- N represents the number of individuals.

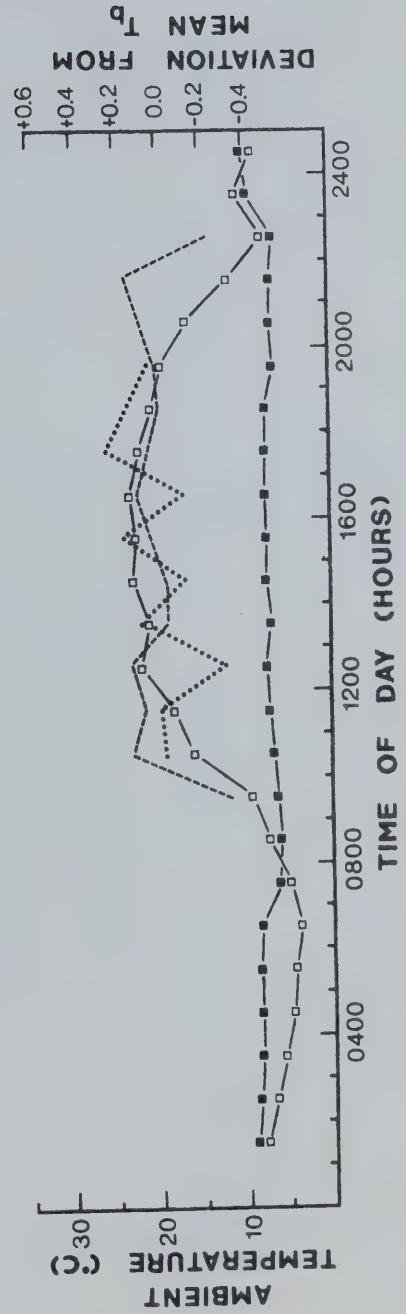
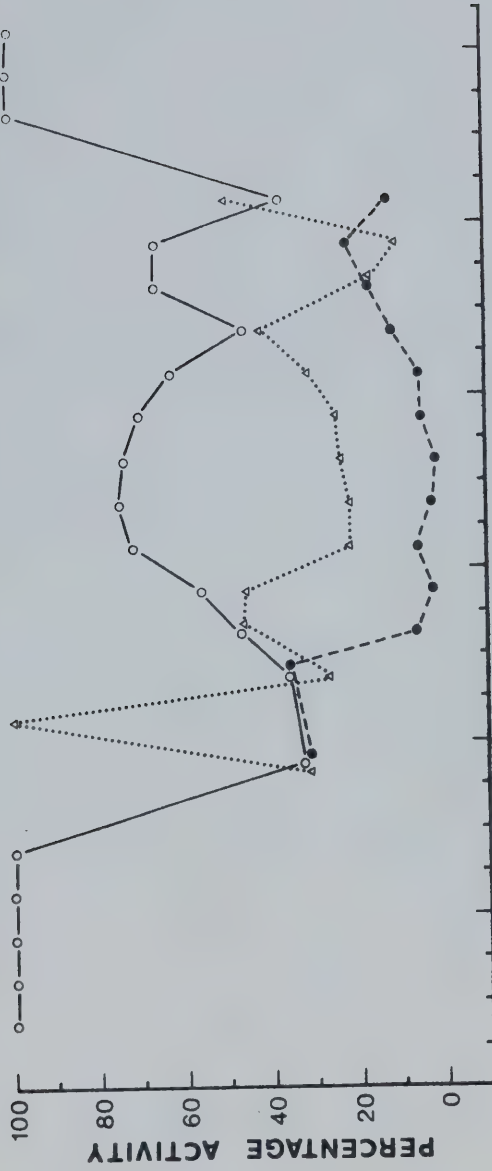






Figure 17. Percentage of total observations of *O. princeps* on the surface of the rocks in relation to weather.

- - Cool, cloudy weather conditions - occasional sunny periods; some light drizzle. Surface  $T_a = 5-15$  C (N = 7; 62 measurements)
- - Warm, sunny weather conditions - occasional cloudy periods. Surface  $T_a = 20-30$  C (N = 7; 157 measurements)

N represents the number of individuals.

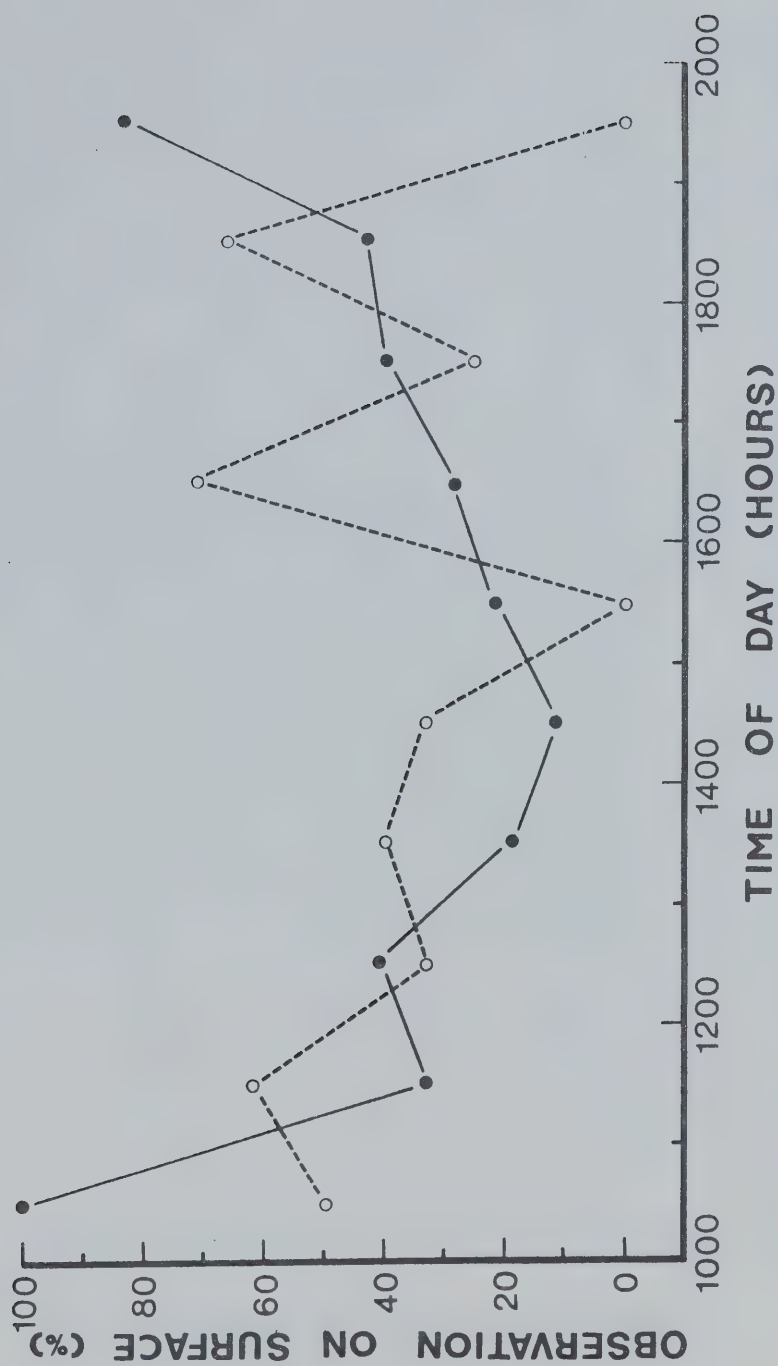








Figure 18. Mean hourly ambient temperatures in rockslide. Sheep River study area, June 4-24; July 12-August 9, 1972.

- - Probe 1 - 0.8 m below surface
- - Probe 2 - 0.9 m below surface
- ▲ - Probe 3 - surface of rockslide
- △ - Probe 4 - 1.4 m below surface
- - Probe 5 - haypile site
- - Probe 6 - haypile site

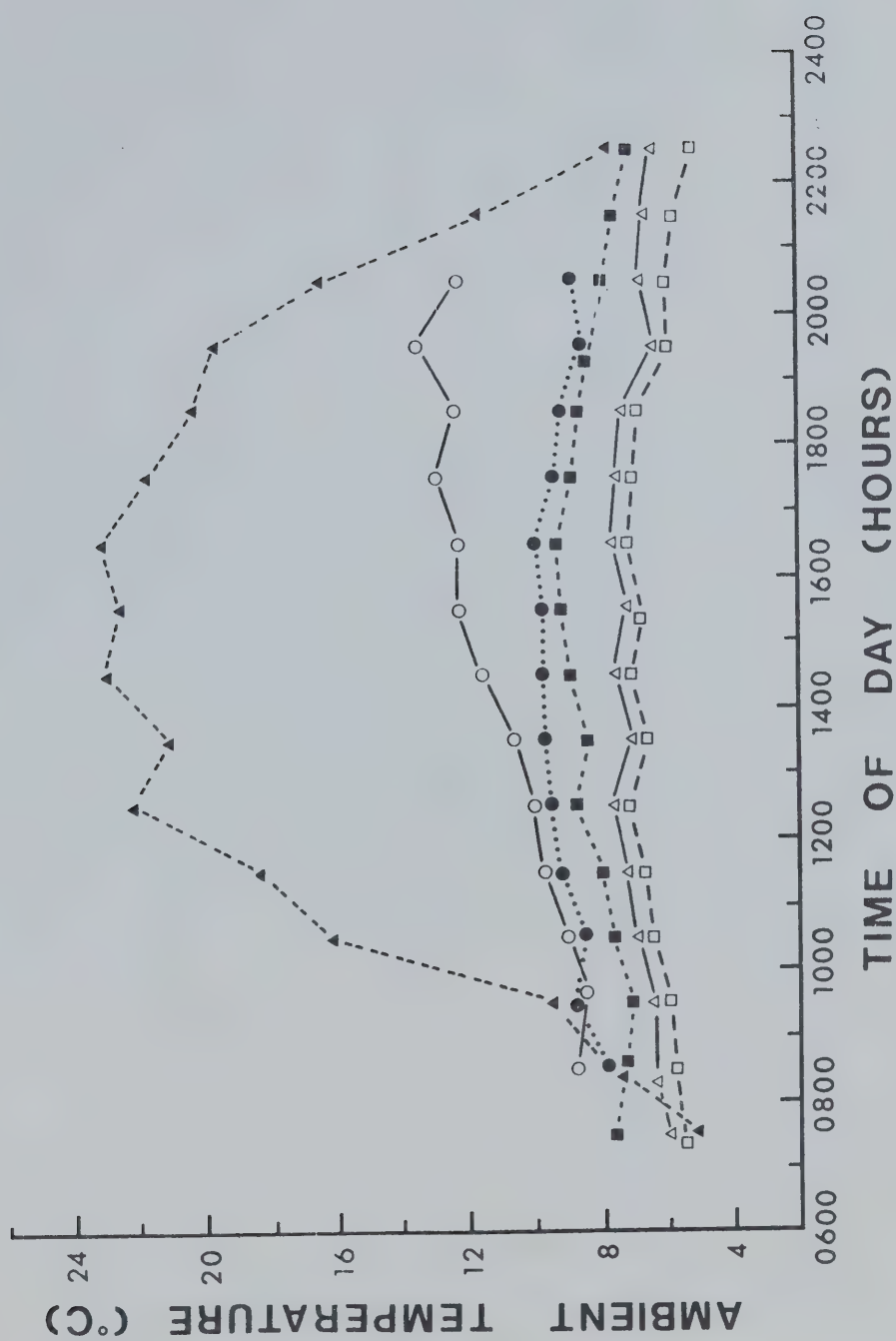






Figure 19. A representative 24-hour record of rockslide ambient temperatures. Sheep River study area, August 2-3, 1972.

- ..... - Mercury thermometer - 0.8 m above surface
- - Probe 1 - 0.8 m below surface
- - Probe 2 - 0.9 m below surface
- ▲ - Probe 3 - surface of rockslide
- △ - Probe 4 - 1.4 m below surface
- - Probe 5 - haypile site
- - Probe 6 - haypile site









Figure 20. Minimum oxygen consumption of *O. princeps* at different ambient temperatures (N = 16; 103 measurements). Minimal and maximal estimates of thermal conductance are fitted by eye. N represents the number of individuals.

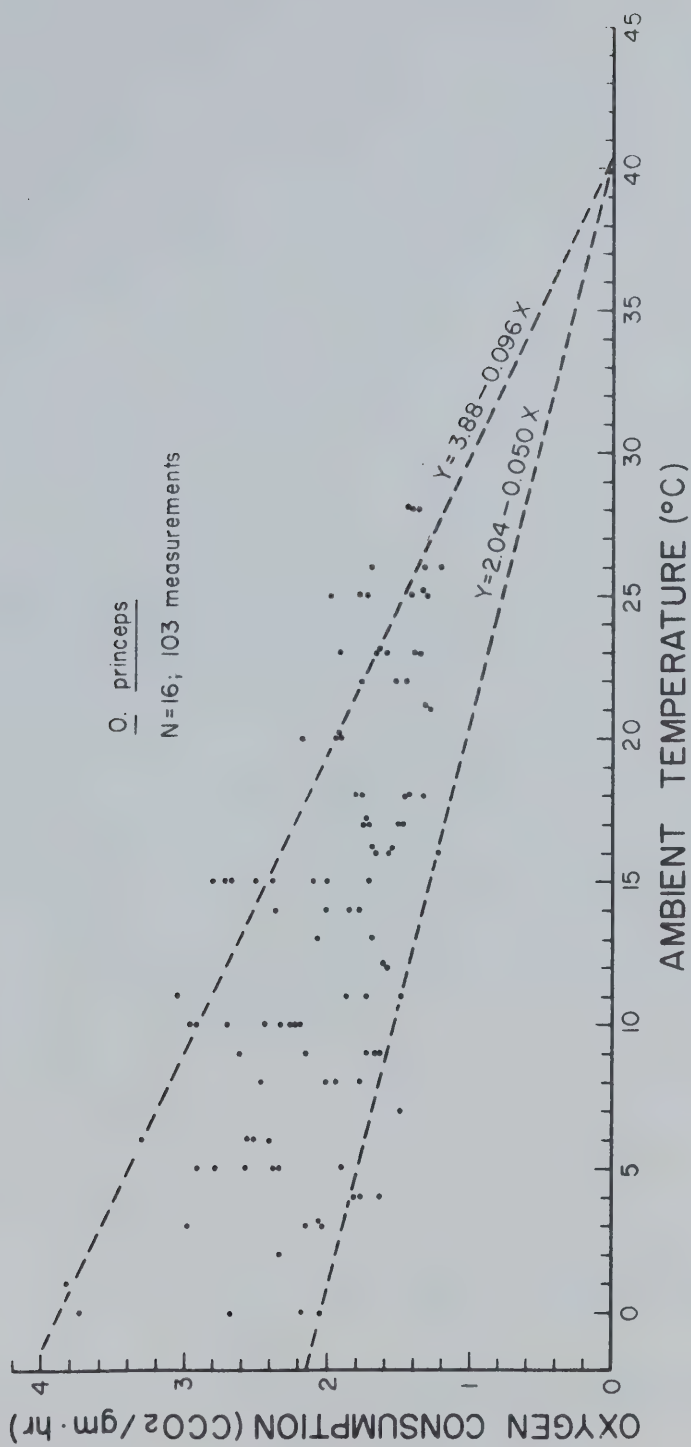


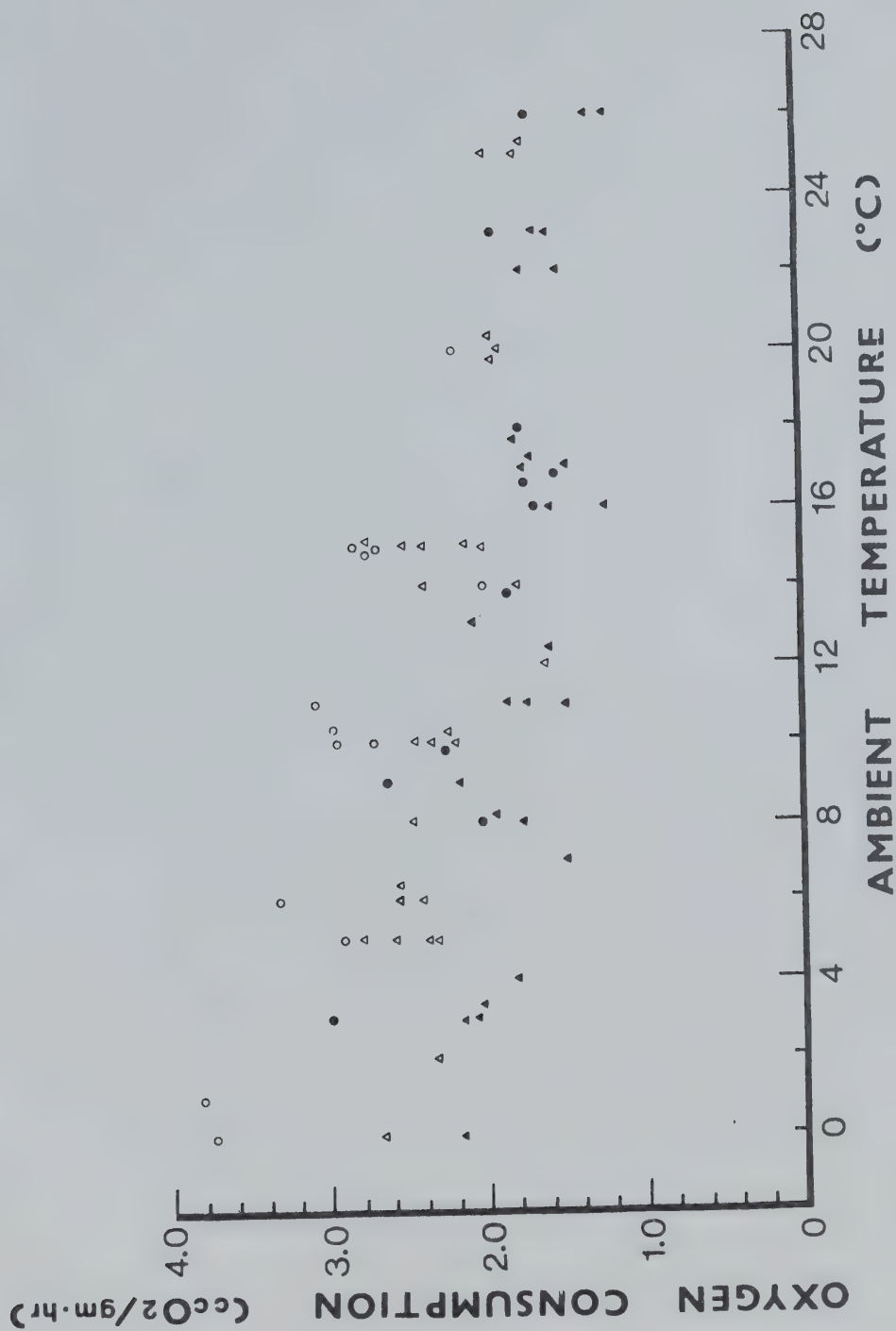




Figure 21. Minimum oxygen consumption of non-acclimated and acclimated *O. princeps* at different ambient temperatures (N = 16; measurements).

- △ - Non-acclimated adults
- ▲ - Acclimated adults
- - Non-acclimated juveniles
- - Acclimated juveniles

N represents the number of individuals.















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